SHOUT
SHARE
IT

THE UNIVERSITY
OF ILLINOIS
LIBRARY

NATURAL HISTORY SURVEY

570.5
ILL
v.4 cop.4

Return this book on or before the *Latest Date* stamped below. A charge is made on all overdue books.

U. of I. Library

MAR 27 1939
MAY 29 1939

11148-S

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. IV July, 1917 No. 1

LIFE HISTORY STUDIES ON MONTANA TREMATODES

BY

ERNEST CARROLL FAUST

Price $2.00

PUBLISHED BY THE UNIVERSITY OF ILLINOIS
UNDER THE AUSPICES OF THE GRADUATE SCHOOL
URBANA, ILLINOIS

UNIVERSITY OF ILLINOIS STUDIES PUBLISHED

ILLINOIS BIOLOGICAL MONOGRAPHS

THE ILLINOIS BIOLOGICAL MONOGRAPHS is a serial published quarterly by the University of Illinois. It is the purpose of the publication to present in monographic form research contributions of especial merit and of somewhat extended character. Each volume will include about 500 pages and 20 or more full page plates. The series may be obtained at a subscription price of three dollars yearly. Individual numbers will be sold separately at prices determined by the size and amount of illustration contained in the particular number.

Vol. I

Nos. 1 and 2. A Revision of the Cestode family Proteocephalidae. With 16 plates. By G. R. La Rue. $2.00.

No. 3. Studies on the Cestode family Anoplocephalidae. With 6 plates. By H. Douthitt. 80 cts.

No. 4. Some North American Larval Trematodes. With 8 plates. By W. W. Cort. $1.20.

Vol. II

No. 1. Classification of Lepidopterous larvae. With 10 plates. By S. B. Fracker. $1.50.

No. 2. On the Osteology of some of the Loricati. With 5 plates. By J. E. Gutberlet. 50 cts.

No. 3. Studies on Gregarines, including twenty-one new species and a synopsis of the Eugregarine records from the Myriapoda, Coleoptera, and Orthoptera of the world. With 15 plates. By Minnie E. Watson. $2.00.

No. 4. The Genus Meliola in Porto Rico. With 5 plates. By Frank L. Stevens. 75 cts.

Vol. III

No. 1. Studies on the factors controlling the rate of regeneration. By Charles Zeleny. $1.25.

No. 2. The head-capsule and mouth-parts of Diptera. With 25 plates. By Alvah Peterson. $2.00.

No. 3. Studies on North American Polystomidae, Aspidogastridae, and Paramphistomidae. With 11 plates. By Horace W. Stunkard. $1.25.

No. 4 Color and color-pattern mechanism of Tiger Beetles. With 29 black and 3 colored plates. By Victor E. Shelford. $2.00.

Vol. IV

No. 1. Life history studies on Montana Trematodes. By E. C. Faust. With 9 plates. $2.00.

UNIVERSITY OF ILLINOIS STUDIES IN LANGUAGE AND LITERATURE

The Studies in Language and Literature are designed to include monographs in general linguistics and comparative literature; the classical languages and Sanskrit; the Romance languages; and English, the Scandinavian, and other Germanic languages. The title of the series will be so construed as to admit the publication of such researches in the history of culture as may throw light on the processes of language and the interpretation of literature. This series is published quarterly; the annual subscription price is three dollars.

Vol. I

Nos. 1 and 2. The phonology of the dialect of Aurland, Norway. By G. T. Flom. $1.25.

Nos. 3 and 4. Studies in the Milton tradition. By John Walter Good. $1.75.

Vol. II

No. 1. Thomas Warton: a biographical and critical study. By Clarissa Rinaker. $1.00.

No. 2. Illustrations of medieval romance on tiles from Chertsey Abbey. By Roger Sherman Loomis. 75 cts.

No. 3. Joseph Ritson: a critical biography. By Henry Alfred Burd. $1.15.

No. 4. Miscellanea Hibernica. By Kuno Meyer. $1.00.

Entered as second-class matter July 27, 1915, at the post-office at Urbana, Illinois, under the act of August 24, 1912

UNIVERSITY OF ILLINOIS STUDIES IN LANGUAGE AND LITERATURE.—Continued.

Vol. III

No. 1. The *Ad Deum Vadit* of Jean Gerson. By David Hobart Carnahan. $1.75.

No. 2. Tagalog Texts with grammatical analysis. Part I. Texts and translation. By Leonard Bloomfield. $1.50.

No. 3. The same. Part II. Grammatical analysis. By Leonard Bloomfield. $3.00.

No. 4. The same. Part III. List of formations and glossary. By Leonard Bloomfield. $1.50.

Vol. IV

No. 1. Madame de Staël's literary reputation in England. By Robert C Whitford. 75 cts.

No. 2. Index verborum quae in Senecae fabulis necnon in Octavia Praetexta reperiuntur a Guilielmo Abbott Oldfather, Arthuro Stanley Pease, Howardo Vernon Canter confectus. (In press.)

UNIVERSITY OF ILLINOIS STUDIES IN THE SOCIAL SCIENCES

The University of Illinois Studies in the Social Sciences are designed to afford a means of publishing monographs prepared by graduate students or members of the faculty in the departments of history, economics, political science, and sociology. Each volume will consist of about 600 printed pages annually. The subscription price is three dollars a year.

Vol. I

Nos. 1 and 2. Financial history of Ohio. By E. L. Bogart. $1.80.

No. 3. Sources of municipal revenues in Illinois. By L. D. Upson. *Out of print.*

No. 4. Friedrich Gentz: an opponent of the French revolution and Napoleon. By P. F. Reiff. 80 cts.

Vol. II

No. 1. Taxation of corporations in Illinois, other than railroads, since 1872. By J. R. Moore. 55 cts.

Nos. 2 and 3. The West in the diplomatic negotiations of the American Revolution. By P. C. Phillips. $1.25.

No. 4. The development of banking in Illinois, 1817–1863. By G. W. Dowrie. 90 cts.

Vol. III

Nos. 1 and 2. The history of the general property tax in Illinois. By R. M. Haig. $1.25.

No. 3. The Scandinavian element in the United States. By K. C. Babcock. *Out of print.*

No. 4. Church and state in Massachusetts, 1691–1740. By Susan M. Reed. $1.05.

Vol. IV

Nos. 1. The Illinois Whigs before 1846. By C. M. Thompson. 95 cts.

No. 2. The defeat of Varus and the German frontier policy of Augustus. By W. A. Oldfather and H. V. Canter. 75 cts.

Nos. 3 and 4. The history of the Illinois Central railway to 1870. By H. G. Brownson. $1.25.

Vol. V

No. 1. Enforcement of international law by municipal law in the United States. By Phillip Quincy Wright. $1.25.

No. 2. The life of Jesse W. Fell. By Frances M. Morehouse. 60 cts.

No. 3. Land tenure in the United States with special reverence to Illinois. By Charles L. Stewart. 75 cts.

No. 4. Mine taxation in the United States. By L. E. Young. $1.50.

UNIVERSITY OF ILLINOIS STUDIES IN THE SOCIAL SCIENCES.—Continued.

Vol. VI

Nos. 1 and 2. The veto power of the Governor of Illinois. By N. H. Debel. $1.00.
No. 3. Wage bargaining on the vessels of the Great Lakes. By H. E. Hoagland. $1.50.
No. 4. The household of a Tudor nobleman. By P. V. B. Jones. $1.50.

UNIVERSITY STUDIES

General Series, Vol. I, II, and III

Partly out of print. A detailed list of these numbers will be sent on request.

Vol. IV

No. 1. The origin of the land grant of 1862 (the so-called Morrill act) and some account of its author, Jonathan B. Turner. By E. J. James. Cloth $1.35; paper 75 cts.
No. 2. Fragment RA.58C of Konongs Skuggsja, from an old Norwegian parchment codex of the XIIIth century, with heliotype copy and a study of the paleography and the language. By G. T. Flom. $1.25.
No. 3. Michel-Jean Sedaine: Le philosophe sans le scavoir. Variorum critical edition, based upon the second Paris edition of 1766 and its appendix with an introduction treating of all known editions and translations. By T. E. Oliver. $1.75.

PUBLICATIONS OF THE UNIVERSITY OF ILLINOIS

Following is a partial list of the publications issued at the University:

1. The University of Illinois Studies in Language and Literature. Published quarterly. Three dollars a year.

2. The University of Illinois Studies in the Social Sciences. Monographs in history, economics, political science, and sociology. Quarterly. Three dollars a year.

3. The Illinois Biological Monographs. Quarterly. Three dollars a year.

4. The University Studies. A series of monographs on miscellaneous subjects.

5. The Journal of English and Germanic Philology. Quarterly. Three dollars a year.

For any of the above address 156 Administration Building, Urbana, Illinois.

6. The Bulletin of the Engineering Experiment Station. Reports of thee research work in the Engineering Experiment Station. Address Director of Engineering Experiment Station, University of Illinois.

7. The Bulletin of the Agricultural Experiment Station. Address Director of Agricultural Experiment Station, University of Illinois.

8. The Bulletin of the State Laboratory of Natural History. Address Director of State Laboratory of Natural History, University of Illinois.

9. The Bulletin of the State Geological Survey. Address Director of State Geological Survey, University of Illinois.

10. The Bulletin of the State Water Survey. Address Director of State Water Survey, University of Illinois.

11. The Report of the State Entomologist. Address State Entomologist, University of Illinois.

12. The Bulletin of the Illinois Association of Teachers of English. Address 301 University Hall, University of Illinois.

13. The Bulletin of the School of Education. Address 203 University Hall, University of Illinois.

14. The Law Bulletin. Address 207 Law Building, University of Illinois.

15. The general series, containing the University catalog and circulars of special departments. Address The Registrar, University of Illinois.

ILLINOIS BIOLOGICAL MONOGRAPHS

PUBLISHED QUARTERLY
UNDER THE AUSPICES OF THE GRADUATE SCHOOL
BY THE UNIVERSITY OF ILLINOIS

VOLUME IV

Urbana, Illinois
1918-1919

Editorial Committee

Stephen Alfred Forbes
William Trelease
Henry Baldwin Ward

570.5
ILL
v.4
cop.4

TABLE OF CONTENTS

VOLUME IV

NUMBERS		PAGES
1	Life History Studies on Montana Trematodes. By Ernest Carroll Faust. With 9 plates and one text figure	1-120
	(Distributed March 6, 1918)	
2	The Goldfish (*Carassius carassius*) as a Test Animal in the Study of Toxicity. By Edwin B. Powers. With graphs and tables	121-194
	(Distributed July 28, 1918)	
3	Morphology and Biology of Some Turbellaria from the Mississippi Basin. By Ruth Higley. With 3 plates	195-288
	(Distributed December 31, 1918)	
4	North American Pseudophyllidean Cestodes from Fishes. By Arthur Reuben Cooper. With 13 plates	288-542
	(Distributed May 31, 1919)	

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. IV July, 1917 No. 1

EDITORIAL COMMITTEE

STEPHEN ALFRED FORBES WILLIAM TRELEASE

HENRY BALDWIN WARD

PUBLISHED UNDER THE
AUSPICES OF THE GRADUATE SCHOOL BY
THE UNIVERSITY OF ILLINOIS

Copyright by the University of Illinois 1918
Distributed March 6, 1918

LIFE HISTORY STUDIES ON MONTANA TREMATODES

WITH 9 PLATES AND
1 TEXT FIGURE

BY
ERNEST CARROLL FAUST

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward, No. 98

732173

THESIS

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1917

TABLE OF CONTENTS

	Pages
Introduction	7
Methods of Investigation	7
Biology of the Bitter Root Valley	9
Morphology of Trematodes Found	13
Introduction	13
Embryology	14
Parthenitae (Sporocyst and Redia)	18
Cercaria General	23
Integument	27
Parenchyma	29
Musculature	30
Armature	31
Glands	32
Excretory System	36
Digestive System	43
Genital System	44
Nervous System	47
Description of the Trematodes Infecting Mollusks of the Bitter Root Valley	57
Introduction	57
Monostomata	58
Cercaria pellucida Faust 1917	58
Cercaria konadensis Faust 1917	61
olostomata	62
Cercaria flabelliformis Faust 1917	62
Tetracotyle pipientis nov. spec	64
Cercaria ptychocheilus Faust 1917	66
Distomata	68
Xiphidiocercariae	68
Cercaria crenata Faust 1917	68
Cercaria glandulosa Faust 1917	69
Cercaria diaphana Faust 1917	71
Cercaria dendritica Faust 1917	72
Cercaria micropharynx Faust 1917	74
Cercaria racemosa Faust 1917	75
Echinostome Cercariae	76
Cercaria trisolenata Faust 1917	76
Cercaria biflexa Faust 1917	78
Furcocercariae	80
Cercaria gracillima Faust 1917	80
Cercaria tuberistoma Faust 1917	82
Pathology	84
Problems Presented	86
Interrelation of Trematodes	86
Relation of Trematodes to Other Groups	90
Life Cycle of the Digenetic Trematodes	92
Summary	94
Species Described in this Paper	95
Bibliography	96
Explanation of Plates	102

INTRODUCTION

During a two years' residence at Missoula, Montana, from 1914 to 1916 the writer became acquainted with the biology of the inter-mountain region of the Bitter Root valley. The heavy trematode infection of the animals in this locality has led to an investigation of the life history of the trematodes of the region.

An opportunity is taken at this place to express appreciation to all who have aided in this study, but especially to Professor Henry B. Ward whose kindness and sincere interest have made the work possible.

METHODS OF INVESTIGATION

This study is confined to the trematodes infecting mollusks. The majority of the collections were made by Mr. Norbert Sager of Missoula. A sketch map (text-fig. 1) indicates the location of each collection. The snails were shipped in damp green moss and arrived in excellent condition.

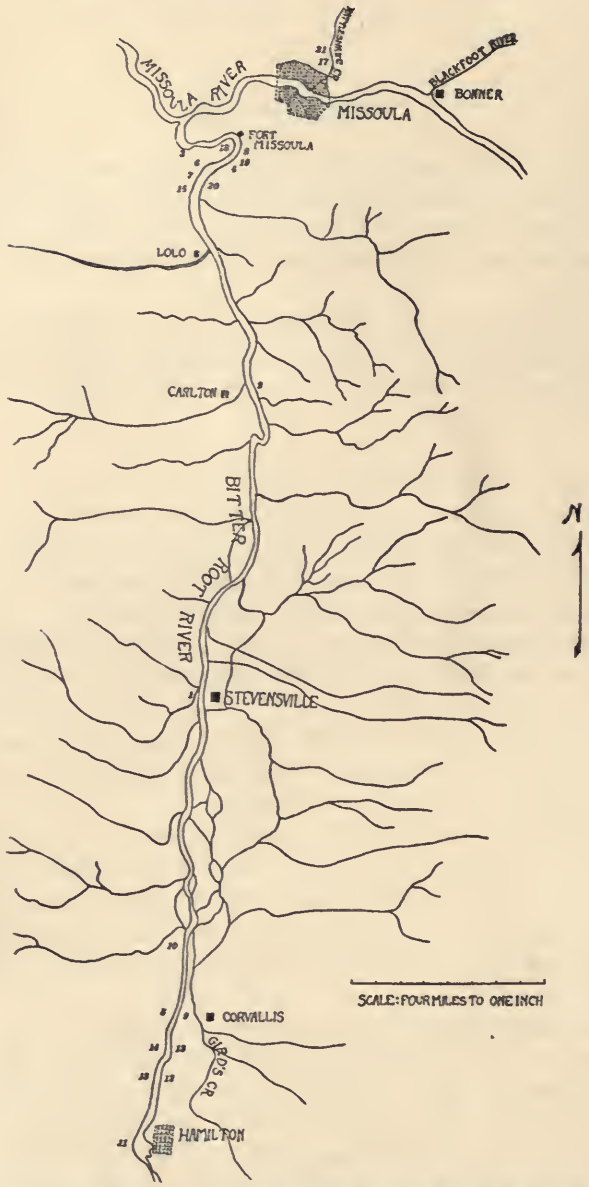
These observations on living material gave data on the stages of development within the mollusk, on the methods of locomotion, on encystment, and on the excretory system.

The worms were removed from the infected tissue and placed in a watch glass in 0.3 per cent saline solution. The change from the host tissue to the saline medium usually caused rapid movement.

It is essential that the excretory system be studied in the living material as, aside from the vesicle and the main trunks of this system, very little can be made out in the preserved material. The delicate structure of the flame cells and the finer capillaries makes it necessary that these organs be examined in living specimens, for in fixation they are likely to collapse, even with the most careful technic.

The organs of the digestive system come out equally well in living and preserved mounts. Some systems, as a rule, can be made out only from preserved and stained material. The most important of these is the genital complex. For all ordinary purposes the material was fixed in Gilson's reagent, altho equally good results were obtained from a corrosive-acetic fixing agent. From the preserved material toto mounts and sections were made, using Delafield's hematoxylin and Ehrlich's acid hematoxylin as stains. A strong counter-stain of eosin in the sections brought out remarkably well the nerve fibers of the worms. Wax models were made of the mature and immature stages of the nervous system of cercariae and parthenitae.

Care was taken to keep the mounts acid-free, and for that purpose all reagents except the destaining fluid were made slightly alkaline with dessicated



Text-figure 1. Sketch map of the Bitter Root Valley, Montana, showing localities where collections were made.

potassium acetate. Some specimens were fixed without any acid fraction in the reagent in order to preserve the excretory granules. These granules, as well as the mucoid cyst membrane of the encysted worm, gave beautiful biuret and xanthoproteic reactions, suggesting a tyrosine compound.

BIOLOGY OF THE BITTER ROOT VALLEY

The snails commonly found in the Bitter Root valley are *Physa gyrina* Say, *Lymnaea proxima* Lea, and *Planorbis trivolvis* Say. They have been identified by Mr. Bryant Walker of Detroit, Michigan. All of these snails were collected from the lower part of the valley, but *Planorbis trivolvis* was not found in the upper reaches of the river. These mollusks are the hosts of the trematodes considered in this paper.

Two facts stand out predominantly in the study of these parasites: the large number of species of trematodes in the snails in the limited range of the valley, and the high per cent of infection both among individuals of a species and within the individual of the species.

There have been found in a single season's collection thirteen trematode species in the snails of the valley, and one larval trematode in the squaw-fish, *Ptychocheilus oregonensis* Richardson. A total of fifteen collections of snails was made during the fall of 1916 and four collections during May 1917. Seventeen of these collections contained trematode infection. *Lymnaea proxima* was taken eight times from five different localities, *Physa gyrina* was taken eleven times from eight different localities, and *Planorbis trivolvis* was taken three times from two localities (Table I, see next page).

The infection record shows that the host is not specific. In the infection of mollusks with *Cercaria pellucida* the host around Buckhouse Bridge was Physa, while that up the valley was Lymnaea. *Cercaria gracillima* was found both in Physa and in Lymnaea in the region of Buckhouse Bridge from different collections. *Cercaria trisolenata* was found both in Physa and in Lymnaea in the region of Buckhouse Bridge and in the vicinity of Fort Missoula. While no parasite species was found in more than two of the three snails common in the valley, there is reason to believe that the third species of snail might be the host under proper conditions. This view is contrasted with that of Thomas (1883:106) who found that only one English mollusk, *Lymnaea trunculata*, "could serve as an intermediate host to the liver fluke," altho this writer suggested that other species of snails must serve in other countries as hosts to the worm. This preference for a particular mollusk in a particular locality, coupled with the ability to select a different molluscan host in another locality, has been found to hold true not only for *Fasciola hepatica*, but also for *Schistosoma haematobium* (Leiper, 1916) and *S. mansoni* (Leiper, 1916; Lutz, 1916; Iturbe and Gonzalez, 1917). When two hosts so different structurally as Physa and Planorbis are equally heavily infected, it seems evident that the stimulus to which the miracidium of the fluke responds can

TABLE I

DISTRIBUTION OF CERCARIAE IN THE BITTER ROOT VALLEY

SPECIES	Stevensville	Carlton	Maclay Sloughs	Fort Sloughs	Corvallis	Buckhouse Bridge	Buckhouse Bridge	Fort Springs	Corvallis	2 mi. below Corvallis	5 mi. above Corvallis	3 mi. above Corvallis	1½ mi. above Corvallis	1½ mi. above Corvallis	3 mi. above Corvallis	Roadhouse	Rattlesnake Creek	Fort Sloughs	Fort Springs	Buckhouse Bridge	Rattlesnake Creek
	NUMBER OF COLLECTION																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Monostomes																					
Cercaria pellucida						a							b								
C. konadensis													b								
Holostomes																					
C. flabelliformis					a				a	a											
C. ptychocheilus	d	d																			
Distomes																					
C. crenata								b													
C. glandulosa											a										
C. diaphana													b								
C. dendritica				b			b														
C. microphárynx																	b				b
C. racemosa							b														
C. trisolenata			a		a	a												b	b		
			c			c															
C. biflexa																a				c	
C. gracillima			a			a	b									a	b	b		a	
C. tuberistoma												a									

a, Physa gyrina b, Lymnaea proxima c, Planorbis trivolvis d, Ptychocheilus oregonensis
Compare with map on page 8.

not be specific. In the case of *Cercaria trisolenata*, where the infection ranged from 22 to 100 per cent in Physa and from 50 to 100 per cent in Planorbis, the host must be considered facultative.

In several instances the same species of snail from the same collection harbored two or more cercariae (cf. collections nos. 3, 6, 7, 13, 16, 17, 18). For example (Table I), at the Maclay Sloughs both *Cercaria trisolenata* and *C. gracillima* were found in the same host species, Physa, in fact in the same individual. This case is paralleled by the record of Cort (1915:55), where the sporocysts of *Cercaria polyadena* and *C. reflexae* were found within the same liver tissue of *Lymnaea reflexa*. However, Ssinitzin (1911) in an examination of several thousand snails of six species, in which he discovered twenty-one species of cercariae, makes no record of two species in the same host individual.

In the collection of *Lymnaea proxima* from Buckhouse Bridge three species of trematodes were found as parasites, *Cercaria dendritica*, *C. racemosa*, and

C. gracillima. In such a case as this, one species, *C. dendritica*, was present in each host in large numbers, while *C. racemosa* was less frequent, and the third species of worm, *C. gracillima*, constituted a very light infection in only one of the thirty-two snails examined. Hausmann (1897:16) in referring to the dominance of one parasite species in the individual host, regards this phenomenon as a biological antagonism.

Turning to the per cent of infection in the snails collected in the fall of 1916 (Table II), a heavy parasitism is found to exist. The data are especially significant when compared with the records of other investigators. Cort (1915) gives detailed data for eleven species of mollusks collected from nine localities. His collections were made in the fall of 1913. The least per cent of individuals infected was 1.4, that for *Pleurocerca elevatum*, secured from the Sangamon River at Mahomet, Illinois. This mollusk contained *Cercaria megalura*. The heaviest infection recorded by Cort was that with *C. isocotylea*, where an 18 per cent infection was found in *Planorbis trivolvis* from Urbana, Illinois. The average infection from Cort's eleven species records is 8.5 per cent. Ssinitzin (1911) has recorded data from twenty-one species of cercariae described by him for the vicinity of the Black Sea at Sebastopol. In many cases his records show a uniquely low parasitism, practically insignificant from a pathological point of view. Out of 1159 individuals of *Rissoa venusta* he

TABLE II

INFECTION RECORD FOR CERCARIAE OF THE BITTER ROOT VALLEY

SPECIES	HOST	EXAMINED	INFECTED	PER CENT
1. Cercaria pellucida	a	18	1	5.5
2. Cercaria pellucida	b	16	5	31.3
3. Cercaria konadensis	b	16	5	31.3
4. Cercaria flabelliformis	a	34	5	14.7
5. Cercaria flabelliformis	a	10	3	30.0
6. Cercaria flabelliformis	a	12	3	25.0
7. Cercaria ptychocheilus	d	6	6	100.0
8. Cercaria crenata	b	22	3	13.6
9. Cercaria glandulosa	a	5	2	40.0
10. Cercaria diaphana	b	16	5	31.3
11. Cercaria dendritica	b	14	5	35.7
12. Cercaria dendritica	b	29	3	10.3
13. Cercaria micropharynx	b	32	18	56.3
14. Cercaria racemosa	b	29	3	10.3
15. Cercaria trisolenata	a	12	12	100.0
16. Cercaria trisolenata	c	1	1	100.0
17. Cercaria trisolenata	a	8	2	25.0
18. Cercaria trisolenata	a	18	4	22.2
19. Cercaria trisolenata	c	2	1	50.0
20. Cercaria biflexa	a	71	5	7.0
21. Cercaria gracillima	a	12	1	8.3
22. Cercaria gracillima	a	18	1	5.5
23. Cercaria gracillima	a	29	5	17.3
24. Cercaria gracillima	a	71	33	46.5
25. Cercaria gracillima	b	32	1	3.1
26. Cercaria tuberistoma	a	19	1	5.3

a, Physa gyrina b, Lymnaea proxima c, Planorbis trivolvis d, Ptychocheilus oregonensis

found only one was infected with *Cercaria cribrata* and one with *C. metentera*, or, in each case, only a 0.06 per cent infection. The heaviest infection found by Ssinitzin among these twenty-one species of parasites was that of *C. zernowi* in *Cardium exiguum*, 7.0 per cent. The average for the twenty-one species is only 1.34 per cent. In the cases of the worms found in *Cerithiolum exile* and *Rissoa venusta*, the percentage of infection is so low that no parasites would have been found had not a large number of snails been collected and examined. The record of Iturbe and Gonzalez (1917) for the cercariae of *Schistosoma mansoni* in Venezuela shows a heavy infection.

The infection in mollusks of the Bitter Root valley is decidedly heavy, altho it varies within wide limits under different factors of place and season. The lowest percentage of infection found was that with *Cercaria gracillima* in *Lymnaea proxima* at Buckhouse Bridge, 3.1. From a different slough in the same locality one month later a 46.5 per cent infection with this species was found in Physa. Thus the percentage of infection is found to fluctuate within a very circumscribed area. The least infection of Physa with *C. gracillima* was from the Maclay Sloughs farther down the River, 5.5 per cent. On the other hand, *C. trisolenata* was found as a hundred per cent infection in both Physa and Planorbis collected from these same sloughs. Taken as a whole the infection average during the fall of 1916 for the Bitter Root mollusks is 29.02 per cent. The average by host species is somewhat different, 24.8 per cent for Lymnaea, 25.16 per cent for Physa, and 75.0 per cent for Planorbis. Leaving Planorbis out of consideration because of the few specimens collected there is an average infection of over 24 per cent in Lymnaea and in Physa. The per cent infection for May 1917 (not included in table II) gives an average of 11.5 for Lymnaea, 16.6 for Physa, and 50.0 for Planorbis.

MORPHOLOGY OF TREMATODES

INTRODUCTION

The progress in the morphological and histological knowledge of larval trematodes is wrapped up in the development of discriminate observation and interpretation on the part of investigators. This has been aided in no small degree by the use of better technic and by better optical equipment, but it is for the most part the observer's own expectation that differences must exist in larvae, and his determination to discover faithfully and accurately such a differentiation of structure, that has brought about progress in this line of investigation. No clearer conception of the change in point of view can be obtained than by a contrast of the statement of La Valette, a worker in the field six decades ago, with the expression of Charles Sedgwick Minot just ten years ago. In his Symbolae ad Trematodum Evolutionis Historiam La Valette (1855:34) recites: "nonnullae Trematodum larvae tam exiguam offerunt differentiam ut discrimina earum characteristica vix commonstari queant." Minot (1897:928) voices the modern point of view in his declaration that "it is not true that all embryos are alike; on the contrary they show class, ordinal, and generic differences from one another."

While the writer fully agrees with the idea that the most natural way of correlating larval trematodes with the adult forms is by a knowledge of their life histories, yet such a correlation is not always possible. Looss (1896) probably had the cercaria of *Schistosoma haematobium* among some of the furcocercariae that came under his observation, yet he was forced to admit (p. 167) that "tous ces efforts ont été, quant a la *Bilharzia* complètement négatifs." The writer has attacked this part of the problem with the idea in mind that not only the fundaments of the adult trematode are found in the mature cercaria, but that even the main descriptive features of the adult trematode are already present, so that the worker can recognize the adult in the larva. While it has been impossible to show species correlations between larva and adult it has been found in the course of the investigation that the larva shows clearly the family features that hitherto have been inferred only by the "blunderbuss method" of life-history investigations.

Probably none of the adult trematodes genetically related to the larvae studied have been described. Moreover, the characters common both to larva and adult have been overlooked in the study of many adult species. The writer has been confronted with the problem as to what characters of the larva are ephemeral and what ones are common to cercaria and adult trematode. A thoro analysis of the groups studied, including Monostomata, Holostomata, and Distomata, gives convincing proof that the most constant systems in larva and adult are the nervous, genital and excretory systems. Such systems and organs as tail, cystogenous glands, and stylet are distinctly larval in nature and may or may not show the same relationship as the natural grouping based on characters common to both larva and adult.

EMBRYOLOGY

"Larval trematode" has been used for any phase of the life-history from the fertilized egg to the adult trematode. This is truly a wrong conception in the light of the observations of investigators from early times down to the present. Workers have recognized sporocyst and redia as "nurse" to the progeny. In other words, they are parthenogenetic individuals. Ssinitzin (1905, 1910, 1911) has made a wise separation of sporocyst and redia on the one hand from the cercaria on the other. He groups the mature sporocyst and redia together under the term *parthenita*, or parthenogenetic mother. This term is used thruout this paper to define the mature sporocyst and redia as distinguished from cercaria or other larval trematode of the hermaphroditic generation.

The homology between cercaria, sporocyst and redia in their early stages of development is recognized by Schwarze (1886:64), who compares his studies on the cercaria's development with those of Schauinsland (1883) on miracidia. Schwarze notes the similarity of the "cuticula," the sloughing off of the epidermis, the location of the solid entoblast, which divides so that a portion comes to lie next to the ectoderm and another part around the gut. He shows that the homology is very apparent. "Die Keimzellen des Embryos entsprechen den Genitalzellen der Cercarie, die etwas abgeplatteten Epithelzellen des Embryo den Meristemzellen der Cercarie." He observes the similarity of the excretory system in miracidia, redia and cercaria, and adds "ferner sind sie ebenfalls mit einem Nervensystem ausgestattet, welches die grösste Aehnlichkeit mit demjenigen der Cercarien hat."

Since the miracidium, redia, and cercaria are not, in last analysis, three parts of one life-history, but more exactly three or more genetically related but complete life-histories, it would not be too much to expect, then, that the origin of germ layers in miracidium, redia, and cercaria would be the same. All three generations arise by the cleavage and development of a single germ cell of mesodermal origin. In the miracidium the cell is always fertilized; in the redia and cercaria it is always parthenogenetic. The observations on the similarity of origin of these cells are extensive, yet mostly isolated, and deserve re-emphasis.

The exact method of development of individuals within the sporocyst or redia has been a matter of diversity of opinion. In general one of two views, budding or parthenogenesis, has been supported by investigators. The earlier writers who considered the origin of the germ balls described them as arising endogenously. Thus Moulinié (1856:132) writes: "les Cercaires naissent, comme nous l'avons vu en parlant des Sporocystes, de gemmes plus ou moins arrondis qui se forment dans l'intérieur de ses derniers lorsqu' ils atteint leur développement normal." Then the question arose whether or not the germ ball arose from the ordinary tissues lining the body cavity of sporocyst or redia, or whether special cells were set apart as a germinal epithelium. Leuckart (1886:113-125) asserts that in all cases germ balls arise only from

those cells which remain unquestionably embryonic. He distinquishes between the condition in rediae and sporocysts, for in the former he found a specialized germinal epithelium, while in the latter all of the cells of the body wall remain undifferentiated in character, and in consequence are capable of germ cell production.

Thomas (1883:119) found for the sporocyst-redia generation of *Fasciola hepatica* that the germ balls which develop into rediae arise in part from germinal cells already present in the embryo (sporocyst), but that "they gain an increase in their numbers by the proliferation of cells lining the body cavity." In the rediae he asserts (p. 125) that the majority of the embryos seem to be formed from the transformation of cells at the posterior end. Cells from the body wall become enlarged, and each of these cells undergoes segmentation, giving rise to a morula. Looss (1892:156, 157) is definitely committed to the view that any portion of the epithelium lining the body cavity is capable of producing germ balls, but, as a matter of fact, only the posterior end (the vegetative end) performs such service. Later in the same paper (p. 167) he speaks of the developmental stages as a metamorphosis composed of several generations, in no sense comparable to parthenogenesis. Haswell (1903:500, 501) describes for the sporocyst of an echinostome larva the development of embryos from a single ovarian mass at the posterior end of the body.

Within more recent years the problem of the origin of germ balls has been centered around the criterion of the formation of polar bodies. Coe (1896: 562) found no polar bodies in the germinal epithelium of the sporocyst and redia of *Fasciola hepatica*. Because Reuss (1903:470) found three small granular bodies attached to the germ balls of *Distomum duplicatum* sporocysts, he concluded that maturation occurred. Tennent's work on *Bucephalus haimaenus* (1906:649) supports the argument in favor of the origin of the germ cell from the walls of the body cavity. After the germ cell passes into the body cavity a "polar body" is cut off. Later Tennent has found that there are three cells in the proximity of the germ cell, two of which seem to be the result of division of the first cell. Rossbach (1906:433) finds no cells which he is willing to call polar bodies. He concludes 1) that the small cells near the epithelium are not polar bodies because their walls are not found in direct continuity with the germ cells; 2) that the cells called polar bodies by Reuss are normally present during development of the germ ball, in miracidia, in sporocysts, in rediae, and even in the ovary of sexually mature trematodes; 3) that they are more abundant in the younger sporocysts and rediae, and 4) that they are present in larger numbers than three's. Finally Cary (1909), in his study of the germ cells of an amphistome sporocyst, has found that the germ balls arise from cells of the body wall which mature without reduction and throw off one polar body.

The contribution to the problem of the meaning of the proliferation of germ balls as described in this paper, is based on the development of the germ cells in the rediae of the holostome, *Cercaria flabelliformis* Faust 1917. In the

anterior part of the mother rediae large germ balls of both rediae and cercariae are present. The germinal epithelium is confined to the posterior fourth of the wall lining the body cavity. In some of the larval rediae within the mother rediae the earlier stages of the history of the germ cells have been studied. This has enabled the writer to secure a series of stages of the germ cells all the way from the probable derivation of the mesoderm tissue from the base of the gut up thru maturation and segmentation.

At a stage in the development of the redia when the archenteron is represented by about eight or ten large vesicular cells (Fig. 45), certain cells are found wandering out from the blind end of the gut and spreading thru the body cavity. Some of these cells come to lie against the wall of the cavity and at first appear as protrusions of the wall; later they seem to constitute a loosely formed inner layer of the wall. Other cells of this type are found free in the body cavity. The majority of these cells that have wandered out from the base of the gut are oval in shape, and have attached to them on one side a small, nodular protrusion, consisting of the film of cytoplasm around a densely granular nucleus.

All of these cells, whether attached to the body wall or not, are to be regarded as germ cells, based on their present structure and future behavior. The small nodules are polar bodies. Figure 46 *H* shows this body in process of formation. The mitotic figure is in the anaphase stage, and was found in a germ cell free in the body cavity of a young daughter redia. These data on the origin of the germ cells from the specialized germinal mass at the blind end of the gut support the thesis of Leuckart (1886:123) and Schwarze (1886: 48, 49), that the cells have preserved their original embryonic character. The fact that the production of the polar body and consequent maturation of the germ cells takes place in cells next to the body cavity as well as in those free in the body cavity, explains the observations of Thomas (1883:115) that some of the cells from which the germ balls are derived are "the germinal cells of the embryo or cells derived from them by division, others are formed by a proliferation of the epithelium lining the cavity of the sporocyst," since these two groups are traceable back to a common origin at the base of the gut.

A description is now given in support of the view that the germ cell is a true ovum. In its unmodified condition the germ cell is moderately inconspicuous, similar in all respects to an undifferentiated parenchyma cell. As it begins to change, the cell enlarges, the cytoplasm becomes granular, with many interstitial vacuoles, and the nucleus comes to have a clearly outlined membrane wall. Frequently the chromatin material is massed into a karyosome (Fig. 46 *A*). The chromatin mass now becomes oblong (*B*) and after considerable growth becomes coiled into a thick skein (*C*). The next stage (*D*) shows the division of the skein into eight chromosomes. These chromosomes arrange themselves in an equatorial plate, and soon show a longitudinal splitting. One of these (*b*) is precocious in its behaviour. It wanders toward the edge of the nucleus and divides (b_1, b_2) while the other seven chromosomes

remain with their halves still in contact. The precocious chromosomes take up positions toward the poles of the cell (*G*). The other chromosomes then divide and migrate to opposite poles (*H*), one of these daughter groups being constricted off as a polar body (*I*). As a result of this process eight chromosomes separate by longitudinal splitting, so that half of each goes into the polar body and half remains in the cell. The polar-body remains in cytoplasmic connection with the ovum while the latter undergoes another division. As in the previous division, simple mitosis occurs. The chromosomes b_1, b_2 precede the others in separation into component halves (*(Fig. 46 I)*. In a late anaphase of this second division (*J*) the polar body may divide, altho this is not always the case.

This second division is not a part of the maturation, for that has been accomplished by the expulsion of the single polar body: hence, it constitutes the first division of the mature ovum. After this (*K*) the polar body is entirely separated from the blastomeres (*L*) and disintegrates. Thus maturation consists of a single mitotic division with the extrusion of a polar body, and takes place without any reduction of chromosomes. In other words, the process is one of true parthenogenesis.

The somatic chromosome count of the developing germ ball is eight, consisting of seven ordinary chromosomes and the precocious individual. In support of this statement is the count of each of the first two blastomeres (*K*, *L*), and the chromosome complex in the late metaphase of an endoderm cell of a morula (*M*). In the latter the count is double, e.g., sixteen, in view of the previous splitting of the chromosomes antecedent to separation into the daughter chromosome groups. The consistent tendency of the chromosome *b* and its descendents to separate from the chromosome mass and to divide before the other seven split, suggests the possibility that this chromosome is a heterosome, two of which Lindner (1914) has found in the adults of *Schistosoma haematobium*.

In the case of the germ balls that never reach the body wall, the process of maturation takes place free in the body cavity. For those cells which lodge against the wall and even fuse with the wall, the process of maturation and cleavage into two blastomeres takes place while the ovum is still in contact with the body wall. At this time it is set free and allowed to develop into a germ ball.

In the older mature rediae (Fig. 44) the epithelial layer of the body wall lining the body cavity consists of a syncytium in which nuclei are arranged irregularly. The cell boundaries become distinct only as maturation of the cells approaches.

Leuckart (1886:124) has stated that it is relatively long after germ ball formation before it is evident whether the embryo is to develop into a redia or cercaria. While the chromosomal history in the rediae of *Cercaria flabelliformis* shows no difference between cells which develop into daughter rediae or cercariae, the cytoplasmic history of this species is indicative of the generation

of the offspring at an early date. The cytoplasm of the germ cells which develop into rediae is granular altho quite transparent. It stains a delicate lavender with Delafield's hematoxylin. On the other hand, from the very outset the cytoplasm of the cercaria type of cell is fibrillar, with many large intermediate vacuoles. It stains a deep magenta with the same dye in the same section as the rediae ova. Figure 46 *L* represents the first cleavage of the cercaria embryo. The chromosome count is identical to that in each blastomere in a redia-forming embryo. Subsequent divisions are difficult to follow on account of the opacity of the cercaria germ-balls. It is very evident, nevertheless, that differentiation of layers and organs takes place much more rapidly in the cercaria ovum than in the redia ovum.

The arguments produced by Rossbach (1906:433), to show that there are no polar bodies given off by the germ cell, do not hold in the case of *Cercaria flabelliformis*. The polar bodies have been found not only in cytoplasmic continuity with the ovum, but in the actual state of mitosis preceding the separation of the polar nucleus from the germ ball. Polar bodies are indeed more numerous in the young rediae, since this is the period when the majority of the germ cells free in the body cavity throw off the polar body and mature. Altho Tennent has found three bodies similar to those designated by authors as "polar bodies," no authentic proof is recorded of more than one polar extrusion in the maturing germ cell of a redia or sporocyst.

In summary, it may be said that the study of the germ cells in the rediae of *Cercaria flabelliformis* supports the thesis that true parthenogenesis takes place here; that the germ cells are traceable to a mesodermal cell mass in the region of the blind end of the gut; that a single polar body is extruded; and that maturation takes place without reduction.

It is not surprising that the details of the germ layers have not been worked out in the fertilized trematode egg, because of the yolk inclusions which obscure developmental stages and no doubt modify the behavior of the segmenting cells. Yet it is regrettable that no attempt at the precise origin of the germinal layers has been made on germ balls within the sporocyst or redia. Without any effort at this exact study of the problem the writer has followed in the living rediae of *Cercaria pellucida* and *C. konadensis*, and in the sporocysts of *C. dendritica* the development of the germ balls from the single mature ova, thru unequal divisions into two, three and five cells, up to the morula stage.

PARTHENITAE (SPOROCYST AND REDIA)

Since the classic work of Thomas (1883) on the life-history of *Fasciola hepatica*, it has been the common custom to define the sporocyst and redia in terms of stages in the life-history of the trematode. The sporocyst is the metamorphosed miracidium, and the redia arises within the sporocyst. The cercaria is the parthenogenetic offspring of the redia and develops into the adult trematode. While this represents a so-called typical life-history, it is

worth while to inquire into the facts and see if the outlined sequence of events is always followed. In some cases the sporocyst is the mother of the cercaria, in which case the redia cycle has been omitted. The accompanying table (III) shows that of the fifteen species treated in this paper eight have cercariae derived directly from the germ cells of the sporocyst. Of the seven remaining, five are known to come from rediae, while the parthenitae of the other two species of larvæ are not known.

TABLE III
GERMINAL EPITHELIUM

	PARTHENITA		NON-LOCALIZED	LOCALIZED
	SPOROCYST	REDIA		
Monostomata				
1. *Cercaria pellucida*		x		x
2. *Cercaria konadensis*		x		rachis
Holostomata				
3. *Cercaria flabelliformis*		x		x
4. *Cercaria ptychocheilus*		?		?
5. *Tetracotyle pipientis*		?		?
Distomata				
Xiphidiocercariae				
6. *Cercaria crenata*	x			x
7. *Cercaria glandulosa*	x			x
8. *Cercaria diaphana*	x		x	
9. *Cercaria dendritica*	x			x
10. *Cercaria micropharynx*	x		x	
11. *Cercaria racemosa*	x			x
Echinostome cercariae				
12. *Cercaria trisolenata*		x		x
13. *Cercaria biflexa*		x		x
Furcocercariae				
14. *Cercaria gracillima*	x			x
15. *Cercaria tuberistoma*	x			x

Types of development are characteristic of certain groups. The Monostomata, Holostomata, and Amphistomata and usually the echinostome cercariae develop within rediae. The xiphidiocercariae and the furcocercariae arise from sporocyst tissue. A considerable modification of a typical life-history, such as is found in *Fasciola hepatica*, is displayed among various groups of Digenea. In 1835 von Siebold described a viviparous monostome larva under the name of *Monostomum mutabile*, in which the miracidium bursts the egg-shell while it is still within the uterus. Within this miracidium, without any metamorphosis into a sporocyst, there develops a single redia. *Schistosoma japonicum* has two sporocyst stages, of which the former is covered with a smooth and the latter with a spinous integument (Leiper and Atkinson, 1915:202). This worm has no redia stage, for the cercariae develop within the secondary sporocyst. Cercariae and rediae develop side by side in the rediae of *Cercaria flabelliformis*.

The sporocyst is much simpler than the redia. It is merely a sac with ectoderm covering, and at times a secretory integument. Occasionally one end is partially muscular. From the inner wall of this sac arise the germ balls

that grow into the parthenogenetic individuals. In the simplest types the germinal cell mass consists of the entire internal layer lying next to the ectoderm. Such a type is seen in *Cercaria diaphana* (Fig. 79), and in *C. microphary nx* (Fig. 94). In the majority of cases, however, the germinal tissue is localized at one end of the sporocyst. In two cases at least there is the differentiation of a muscular attachment organ at the antipodal end (*C. dendritica*, Fig. 87; *C. racemosa*, Fig. 105). In the furcocercariae, *C. gracillima* and *C. tuberistoma* (Figs. 147, 157), there is a rhizoid-like attachment at the germinal end. In these cases there seems to be some evidence for regarding the germinal layer as localized at the end opposite the potential mouth.

The redia is the type of the life cycle normally developing within the sporocyst. Its organization is much more complex than that of the sporocyst. There is a well-developed oral aperture, a muscular pharynx, and a sac-like gut. There is a birth-pore just behind the collar region, on the left side, slightly ventral. Two projections, usually in the posterior part of the body, readily differentiate the redia externally from the shapeless sporocyst. With some justification Ssinitzin (1911:76) regards these projections as comparable to an originally bifid tail of the cercaria as in Bucephalus. In the cephalic region around the pharynx there is a nerve complex of highly differentiated nerve cells and nerve fibers. These are distinguishable as a central nerve ring, with four anterior and four posterior trunks. The posterior trunks do not develop far caudad. The integument is well developed and thick, and muscular layers within it play an important rôle in the movement of the redia, whereas the sporocyst depends almost entirely for its movement on the motility of the larvae within it. In the mature redia the germ tissue is always localized at the posterior extremity of the body.

The development of the germinal tissue of sporocyst and redia has been shown to be the result of the maturation of parthenogenetic eggs. The significant correspondence between the localized germinal epithelium of the parthenita and that of the cercaria may be pointed out here. In most cercariae the male germ cells are aggregated into a definite number of testicular masses, in most cases, two. In the apharyngeal furcocercariae (the probable larvae of the Schistosomatidae) the number of germ masses is larger. The data compiled in Table IV, on the better known Schistosomatidae, show that the number of the testicular follicles varies from four to five in *Schistosoma haematobium*, the mammalian parasite (Looss, 1899:658) to about 134 in *Bilharziella polonica*, the avian parasite. The origin of these testes is not described in any case. In all of the adults the sexes are separate. In *Cercaria gracillima* (Fig. 149) the testicular masses are proliferated from a germinal mass at the posterior extremity of the body, ventral to the excretory bladder. They are numerous; some twenty-four or twenty-five masses are found in this region at this stage of maturity. Moreover, the female cell masses are also present in the species at this larval stage, showing that the animal is not primitively unisexual, but hermaphroditic. It would be only one step further back in the phylogeny of the group to assume that the hermaphroditic cell masses and

TABLE IV

MALE GERM CELLS OF THE BETTER KNOWN SCHISTOSOMATIDAE

SPECIES	*Gigantobilharzia acotylea* Odhner 1910	*Ornithabilharzia kowalewski* (Parona and Ariola) 1896	*Bilharziella polonica* (Kowalewski) 1895	*Bilharziella pulverulentula* (Braun) 1901	*Austrobilharzia terrigalensis* S. J. Johnston 1916	*Schistosoma bomfordi* (Montgomery) 1906
NO. OF TESTICULAR FOLLICLES	many	many	134	110	18–20	61
LOCATION OF TESTES	esophagus to posterior end	chain in posterior quarter of body	entire region behind genital atrium	lateral to zig-zag unpaired gut	second quarter of body	three-sevenths entire body length
HOST	*Larus fuscus*	*Larus melanocephalus*	*Anas boschas* *Anas crecca* *Fuligula cristata*	*Anas querquedula*	*Larus novae-hollandiae*	*Bos indicus*
LITERATURE CITATION	Odhner 1910:383	Parona and Ariola 1896	Kowalewski 1896 Parona and Ariola 1896 Odhner 1912	Braun 1901a:947 Odhner 1912	Johnston 1916: 234	Montgomery 1906a:7
HABITAT	West coast Sweden	Mediterranean Sea	Lemberg, also East coast of Gotland	Dongola, Sudan	Terrigal N. S. Wales	India

MALE GERM CELLS OF THE BETTER KNOWN SCHISTOSOMATIDAE—*Continued*

SPECIES	*Schistosoma indicum* (Montgomery) 1906	*Schistosoma bovis* (Sonsino) 1876	*Schistosoma spindalis* (Montgomery) 1906	*Schistosoma mansoni* (Sambon) 1907	*Schistosoma japonicum* (Katsurada) 1904	*Schistosoma haematobium* (Bilharz) 1852
NO. OF TESTICULAR FOLLICLES	5–9	6–8	6–7	8	6–8	4–5
LOCATION OF TESTES	alternate, zig-zag behind ventral sucker	?	?	limited area	limited area behind acetabulum	anterior one-fourth of body
HOST	*Equus caballus* *Equus asinus* *Bos indicus*	*Bos* spp. *Ovis* spp.	*Bos indicus*	man	man, cat, dog	man *Ceropithecus fuliginosus*
LITERATURE CITATION	Montgomery 1906:20	Sonsino 1876 Montgomery 1906a:14	Montgomery 1906a:10	Leiper 1916:411	Katsurada 1914:367	Looss 1895:181 Leiper 1916:411
HABITAT	India	In cattle, thruout Orient, in sheep, Sicily	India, Sumatra	Africa, Central America, South America, Antilles,	Japan, China,	Africa, Western Asia

the germinal epithelium of the parthenitae arose from a common type of germ cell. In other words, the germ cells of cercariae and parthenitae are homologous. Stages in the phylogenetic development of the germinal epithelium may be outlined thus:

1. Germinal epithelium non-localized. Example, *Cercaria diaphana* (Fig. 79), *C. micropharynx* (Fig. 94). Sporocyst cycle.
2. Germinal epithelium localized; no mouth or suctorial apparatus. Example, *C. glandulosa* (Fig. 67). Sporocyst cycle.
3. Germinal epithelium localized; suctorial disc or attachment organ opposite germinal cell mass. Example, *C. dendritica* (Fig. 87), *C. racemosa* (Fig. 105). Sporcyst cycle.
4. Germinal epithelium localized opposite a true oral aperture, with pharynx and gut present. Example, *C. flabelliformis* (Fig. 43). Redia cycle.
5. Germinal epithelium localized and specialized into two sorts of conjugating germ cells, male and female isogametes. (Theoretical.)
6. Male germ cells proliferated in numbers from the mass of germinal tissue at the posterior end of the body; female germ cells more highly differentiated. Example, *C. gracillima* (Fig. 149). Cercaria stage of hermaphroditic cycle.
7. Germinal cells massed into a small number of specialized glands, called testes and ovaries. Example, *C. pellucida* (Fig. 18). Cercaria stage of hermaphroditic cycle.

CERCARIA (GENERAL)

The cercaria is the offspring of the parthenita. It is a highly specialized individual, homologous to the immature redia or the sporocyst. Its specialization has been accounted for by Ssinitzin (1910:38-56) because of 1) a considerable period of free-swimming life, during which it acquired a tail, and 2) a change to parasitism in the vertebrate, which was at first facultative, but later became obligatory. There are two types of modified characters to be accounted for in the cercaria, in addition to the original characters common to parthenita and cercaria. The tail, the well-developed muscle complex, the nerves innervating the muscle system, together with the salivary glands and the sensory papillae—all of these bear evidence of a long period of independent life. When the organism became parasitic, first ectoparasitic, later endoparasitic, the highly developed muscular suckers with their nerve tracts were further developed, while the stylet organs and cystogenous glands were differentiated. The muscular specialization was of primary importance within the host, while the cyst served to protect the worm during the period of transfer from larval to definitive host.

The cercaria varies in size, altho it is fairly constant for a particular family or genus. Holostome larvae reach a size of 0.63 mm. in length and 0.35 mm. in width (*C. ptychocheilus*). On the other hand some of the xiphidiocercariae are much more minute, 0.18 mm. in length by 0.09 mm. in width (*C. micropharynx*).

There are two types of movement in the cercaria aside from the apparent contraction and expansion of the body. One of these is concerned with the forward movement of the animal and depends on the coöperative action of the suctorial organs and the general bodily musculature. The other is caused by the flagellate action of the tail. The movement of the cercaria along a forward path reminds one of the rythmic action of a measuring worm. The oral sucker is always used as one organ of attachment, and the ventral or caudal suctorial disc supplies the other anchorage. With these two organs of attachment, the larval worm applies the oral disc to the object of contact, while it draws the posterior portion of the body forward by the contraction of all the longitudinal muscles. This places the posterior attachment advantageously near the oral disc, so that a relaxing of the longitudinal muscles and a synchronous contraction of the transverse muscles throws the cephalic portion of the worm far forward. In the forms with well developed musculature, such as monostome and echinostome species, the larva may appear discoid on contraction, while the expanded worm will assume a length several times that of the normal body.

All groups of cercariae possess an oral suctorial organ. For the second attachment organ there is a variety of accommodation. Undoubtedly the most advantageously formed organ of this second type is the one found in the Amphistomata, where there is a powerful suctorial disc at the posterior end of the body.

Among the distomes there are many types of posterior suctorial organ, ranging from those with a prominent acetabulum not far from the caudal extremity, as in *Stomylotrema pictum* (Crep.) (Looss 1899:629), to those with a poorly developed acetabulum more cephalic in position. In the latter case there are frequently found auxiliary locomotor organs, such as those in the posterior pockets of the xiphidiocercariae. In some species there is only a suggestion of a paired suctorial organ, as in the larvae, *Cercaria crenata* (Fig. 55), and *C. diaphana* (Fig. 76). In others there is the additional spinose complement (*C. glandulosa, C. dendritica, and C. micropharynx*). These spines are of important function on rough surfaces where the disc can take hold with difficulty. Altho there is considerable difference in the rapidity of movement of the various species studied, *C. glandulosa* was by far the most rapid in movement of all the cercariae observed. The spinous outgrowth of the acetabulum is of advantage in locomotion, catching hold where the unarmed sucker can not operate (*C. glandulosa*, Fig. 60; and *C. gracillima*, Fig. 142).

Muscular development in the holostome larva is confined entirely to the suctorial apparatus, since there is no distinct tail portion. This type of sucker is derived from the distome type. With the translocation of the genital opening to the posterior end of the body, the primitive genital pore has come to be used as an accessory suctorial organ (*Cercaria ptychocheilus*, Fig. 47). The most unique modification is found in the tetracotyle type. Here there have arisen two lateral accessory suctorial grooves (Fig. 41), and lappet modifications of

the acetabulum. All of these come to be enclosed in a common pocket which acts as a large sucking cup (Fig. 40). There is practically no locomotion in these species, since movement is confined almost exclusively to the sucking reflex.

In the monostome no acetabulum is present, yet the cercaria performs the processes of locomotion *par excellence*. The pair of posterior locomotor organs replaces the acetabulum in the measuring worm movement. In *Cercaria pellucida* and *C. konadensis*, as well as in *C. urbanensis* Cort, these organs consist of posterior inpocketings of the integument. In *C. imbricata*, Looss (1896, Fig. 151) there is an internal pocket. In *C. ephemera* Nitzsch (Ssinitzin, 1905, Fig. 75, 76) there are hook-shaped spines. Cort (1915:15) finds that they "apparently have no suctorial function, since no muscles are present and the central cavity contracts while the projection is extended." A careful study of living and preserved specimens of *C. pellucida*, *C. konadensis*, and *C. urbanensis* shows that these three American species have no spinose or other integumentary modifications. However, their function is found to be distinctly suctorial, and not "analogous to setae," as Cort believes. Typical drawings for the locomotor organs of any of these three species are shown (Figs. 16, 17). As will be seen in figure 16, there are four muscles which are attached to the pockets. By a contraction of the pair *xx* the pocket disc is applied to the surface of the contact body; by a relaxation of *xx* and a contraction of *yy* the pocket is released and pulled forward by the general bodily contraction. This has been observed repeatedly in so convincing a manner that it leaves no doubt as to the structure or function of the organ. In addition, in *C. konadensis* (Fig. 21) a group of glands just anterior to the locomotor pockets pour out a mucous secretion at the time when the disc is applied to the contact organ. The locomotor pockets perform a similar function and in a similar manner to that of the secondary suctorial disc or acetabulum of amphistome or distome, altho these organs are in no sense homologous.

The significance of the spines in connection with the caudal locomotor pockets of distomes has been regarded by Leuckart (1886:128) as deserving special consideration. In *Cercaria armata* he considers them as serviceable in keeping the tail attached to the body after the constriction between the two parts has become deep. Looking into the phylogenetic significance of the spines of the same cercaria species, Ssinitzin (1911:68) regards them as indicating a bifid ancestral appendage of a caudal nature. In view of the fact that these pockets actually function similarly to the locomotor pockets of the monostomes, and are more than likely the ancestors of the monostome type of pocket (Fig. 12), it seems hardly worth while to find a more obscure meaning in the structures.

The tail is the portion of the cercaria showing preëminently the adaptation of the organism to free-swimming life. In such forms as *C. setifera* (Monticelli, 1914), *C. pennata* and *C. plumosa* (Ssinitzin, 1911, Figs. 76-79), the prolonged free-swimming existence has given rise to setae, spines and scutes.

The tail arises as a median posterior protuberance, bilaterally symmetrical, and is, according to the views of Ssinitzin, phylogenetically a paired organ. This thesis is supported, in part at least, by the fact that the excretory trunks arise as paired organs in both the body and the tail. In the furcocercariae the caudal tubules remain separate in the rami of the tail and also in the "eyelet anastomosis" at the junction of the body and the tail. There develops in the tail the usual complement of muscles, a transverse layer externally and a longitudinal group more median. Within the cylinder of muscles is the group of parenchyma cells surrounding the excretory tubule.

In the tails of distome cercariae (Figs. 99, 133) the excretory vessel is a paired structure, separated in the middle by a parenchymatous partition with one or two nuclei in each section of 7 μ thickness. Some schistosomatid larvae have, in addition, eleven or twelve pairs of oblong cells just lateral to the excretory vessel. The tail of the monostome is characterized by extra large longitudinal muscles with prominent nuclei. The portion within the longitudinal muscle cylinder differs in structure in individual species. In *C. pellucida* there is one ring of very large parenchyma cells situated around the excretory vessel. There are eight to ten cells to each transverse plane of 7μ. In *C. konadensis* and *C. urbanensis* there are glandular cells within the parenchyma ring; they are large and crowded with granules. In both of these species (Figs. 25, 32) these cells are arranged in six paired groups. In *C. konadensis* there are many cells to each member of the group, arranged in pyramidal fashion with the apex directed distally. Thus the largest cells in each group (Fig. 27) are proximal. These cells lie next to the excretory vessel. Cort has described the cells of *C. urbanensis* thus: "extending the length of the tail and forming a core are two rows of long cells which are close together and have their long axes parallel with the length of the tail. . . . They are full of heavy staining granules. . . There is nothing suggestive of the possible function of these cells." He has failed to observe the exact number of these cells (six pairs) and is in error in considering them as a core extending the whole length of the tail, for they alternate with non-glandular tissue in about half of the extent of the organ. Their structure is probably glandular. In *C. urbanensis* these cells arise from undifferentiated parenchyma cells (Fig. 33). They soon appear as falciform cells in trans-section (Fig. 34), separated in a median sagittal plane by a partition arising between two intermediate parenchyma cells, which soon differentiate into a muscular lamina. The lamina arises before the excretory tubules differentiate as distinct lumina among the parenchyma cells. Thus the bilateral symmetry along the median sagittal plane is well shown. The excretory vessel is single in the mature *C. pellucida* and *C. konadensis*, but remains paired in *C. urbanensis*.

Looss (1893:24-28) cites the epithelial cells of the tail of cercariae as good examples of "Blasenzellen," where all cell elements of the mesenchyme usually become "Blasenzellen", and where no true glands take their place. The study of *C. konadensis*, *C. urbanensis*, and *C. gracillima*, shows that axial cell glands are present, and that they are derived from the parenchyma. Moreover

where these special gland cells are not present, as in *C. pellucida*, the parenchyma cells are more vesicular than where they are present. The writer is in accord with Looss's view that there are no indifferent cells remaining in the tail. Hence the tail, when separated from the body, can not metamorphose into a sporocyst or redia, as the older writers believed (Pagenstecher, 1857:15).

INTEGUMENT

The covering of trematodes and cestodes has been the subject of considerable controversy. Four main theories have been proposed. The Blochmann theory (1896) assumes that the cuticula of trematodes and cestodes is a true morphological cuticula secreted by the hypodermis, as in other invertebrates. A second theory, presented by Brandes (1892), postulates that trematodes have no subcuticula in the true sense of the term, and what has been considered as such is nothing more than the true parenchymatous connective tissue. Nevertheless, the body covering is a true cuticula, secreted by special glandular cells of epidermal origin just beneath the cuticula. The presence of apparent nuclei in the cuticula has revived the old idea of Wagener that the cuticula is a metamorphosed epithelium. Goto has subscribed to this theory in his study of ectoparasitic trematodes (1894:6-13), defining three layers, an outer cuticula, a subcuticula, and a basement membrane. This is also the interpretation Monticelli has put on the body investment of *Cotylogaster michaelis* (1892:189), which he claims to possess an "ectoderma sinciziale di aspetto cuticuloide." More recently Cary (1909:646) has advocated this view. Pratt (1909:721) is inclined toward Leuckart's theory that the cuticula is of parenchymatous origin, a derivative of the peripheral portion of the parenchyma.

The species of larval trematodes studied by the writer are uniform in showing that the epidermal layer, developing into a syncytium in many cases, is present in the early stages of the sporocyst, redia, and cercaria. In the parthenitae, especially in the redia, this layer may persist until the germ balls within are ripe and ready to escape. In the cercaria the epidermal tissue is present in early life as a syncytial layer investing the larva. In the mature cercaria it is sloughed off. The "cuticula," when present, arises from below the epidermis. It is a discrete layer underneath the epidermis, or it impregnates the epidermis from below. In the latter case the nuclei are always superficial, usually rising above the surface as small tuberosities.

In the monostome group, the redia possesses a syncytium of ectodermal cells impregnated here and there with granules of a secretory nature. The cercaria develops a well-defined epidermis which later (Fig. 37) becomes syncytial and is sloughed off. Underneath this the "cuticula" is distinctly cut off from the epidermis on the outside and from the mesodermal tissue beneath. Among the latter are the special parenchyma cells with aciculate pseudopodia, corresponding to Blochmann's "Epithelzellen" (1896:7). These differentiated parenchyma cells have no connection with the "cuticula" in

the developing or mature cercaria of this group. A non-nucleated epidermis is shown in the process of sloughing off for the hemistome cercaria (*C. ptychocheilus*, Fig. 54). Underneath is a distinct layer of "cuticula." Beneath the "cuticula" is a lining of transverse and longitudinal muscle fibers. Median to the complexes of the longitudinal muscles are the complexes of the connective tissue. The whole structure, from the inner wall of the "cuticula" thru to the free parenchyma, is infiltrated and bound together into a single mass by a mucoid secretion. This secretion is indifferent to stains. The epithelial cells of the complex send out long processes toward the integument, so that the processes penetrate into the latter. These cells suggest gland cells, concerned with the secretion of the "cuticula." They are not potentially different from the underlying parenchyma.

Among the distome larvae the writer has studied the "cuticula" problem for echinostomes, schistosomes, and xiphidiocercariae. The redia of *C. trisolenata* possesses an ectodermal reticulum in which are found large vesicular nuclei. This covering is impregnated with large granules which are indifferent to stains. In the cercaria of this form (Figs. 128-133), there is an ectodermal layer present, very thin, with the nuclei arising from the surface as minute tuberosities. Beneath this is the thick layer of "cuticula." The epidermis has been lost in the tail. No "Epithelzellen" are visible in the mesenchyme complex. For the schistosome larva, *C. gracillima*, there are definite nuclei present as minute papillations rising above the surface of the epidermal layer. The sporocyst of this form has no "cuticula." The body wall consists of a single layer of ectoderm cells, arranged end to end, the nuclei of which are oval to subspherical. In the distome, *C. glandulosa*, the sporocyst wall is composed of a single layer of epidermal cells, with falciform nuclei. In the cercaria the epidermis is present only in individuals where the tail is still attached. Here nuclei are present in the peripheral layer of the body, but are not found in the covering of the tail. The "cuticula" is a thin envelope around the circular layer of muscles.

The study of these trematodes with reference to the problem of the integument has led the writer to set aside the view that the "cuticula" is ectodermal in origin, because the ectoderm is superficial, lying outside the "cuticula." The impregnation of this layer with cuticular granules might lead one to believe that the two layers are one, but the earlier history of the layers shows that this conception is erroneous. No hypodermis is found in any of the species studied. Consequently the Blochmann theory can not hold for these species. No special gland cells have been found to support in its entirety the theory of Brandes. On the other hand the evidence of this study points to the sustaining of Leuckart's theory of the parenchymatous origin of the basement membrane on the following grounds. 1) In all the species the basement membrane arises from tissue beneath the ectodermal layer. 2) In all cases where there is an ectodermal layer only (in sporocysts), no basement membrane is found. 3) The heaviest layer is found in species where the parenchyma has a widely diversified potency, such as salivary, cystogenous, locomotor and

mucin glands. 4) The "Epithelzellen" of the monostomes and holostomes (Figs. 37, 54) are characterized by large vesicular nuclei and vacuolated cytoplasm, similar to the "Blasenzellen" of Schwarze (1886) and Looss (1893). They are modified parenchyma cells differing from the underlying layers not in potency but in location. 5) As the secretory cells for the basement membrane, these parenchyma cells have developed long acicular pseudopodia toward the membrane and, in the larval holostomes, have penetrated into it. All of these data point toward the parenchymatous origin of the basement membrane.

PARENCHYMA

Soon after the fundaments of the digestive and nervous systems of the cercaria are laid down, certain cells of mesodermal origin of the germ ball become ovoid and are filled with milky white granules. These are cystogenous cells, the "Stäbenkörnchen" of the German writers and the "cellules à bâtonnets" of the French. They develop most commonly in monostomes, amphistomes, and such distomes as form a heavy cyst.

Other portions of the mesoderm are differentiated as the germinal epithelium and the muscle layers. The remainder of the mesodermal cells is for a considerable time potentially great, and remains undifferentiated (Looss, 1893:29). They constitute the parenchyma. Looss has compared these cells of the mesoderm to the cambium of the plant. They are the "nichtveränderten Zellen," on the multiplication of which depends the growth of the minute larva to the relatively large adult. As the animal grows the cells of this region become more vesicular, vacuoles appear within the cytoplasm, and acidophilous granules appear within the cell. The intercellular spaces become more and more prominent. The cells are held together by bands of ragged connective tissue which, for the most part, is the outgrowth of the interstitial cells. Within this parenchyma complex there appear large tubular lumina in certain definite regions, and, leading into these, tubes and smaller tubules. These are the excretory tubes; at the ultimate ends of these are found the capillaries and the flame cells (Looss, 1892:162; Thomas, 1883:116-118). In the schistosome cercariae studied the main group of cilia is not at the extreme ends of the ducts, but in a pocket in the posterolateral part of the main trunks (Figs. 143, 145). It is of importance to emphasize here that these excretory trunks and tubes are not lined by a wall of specialized cells, but are merely lumina among certain cells of the parenchyma. It seems highly probable that Looss's view is correct as regards the flame or "Trichter," that it, too, is an intercellular lumen, into which the parenchyma-cell cilia protrude, and that it is not in a hollowed-out cell. The cilia are definitely outgrowths of the single cell at the head of the capillary (Fig. 138), a cell which is differentiated from the sister cells of the parenchyma by the possession of a much smaller nucleus and densely granular protoplasm.

MUSCULATURE

The muscle systems of the parthenitae and the cercariae are confined, for the most part, to the peripheral and splanchnic regions. The peripheral muscles consist of an outer series of radial muscle fibers and an inner series of longitudinal fibers. A third series, the dorsoventral, which is common in the adult forms, is suggested at times in the body of the cercaria. The muscles of the intestinal tract consist of a longitudinal and a circular series.

The peripheral system lies directly beneath the basement membrane. It opens interstitially to permit the growth of the processes of the parenchyma cells which secrete the basement membrane. The outermost layer is the circular series. It may consist of a single band one cell in thickness or it may include a cylindrical band several layers thick (Figs. 37, 54, 97, 128). Within this is the longitudinal series. Usually here the individual fibers of the bundles are separated from one another by a considerable interval. The fibers are longer and fewer than those of the circular series. A section of an adult trematode shows, in addition to these, an oblique series of fibers. These oblique fibers give the appearance in section of a diamond pattern. In another type, the dorsoventral, the fibers run at right angles to the frontal plane. In the holostome cercaria (Fig. 54) no such series is found, altho the longitudinal series is so arranged that the fibers are on edge and might be taken for the dorsoventral series. The view of Bettendorf (1897:315, 316) that the "Epithelzellen" of Blochmann are really longitudinal muscles, can not be considered valid, since in the same sections the former are indifferent to stains and the latter are deeply stained by the same methods of technic.

In the oral and acetabular suckers and frequently in the pharynx there exist the transverse, longitudinal and oblique series of muscle fibers, interwoven into an inseparable complex. These are best developed in the Amphistomata. Since the redia which produces germ balls is an adult and the cercaria is an immature individual, it is not surprising that the pharynx of the redia is fibrous, with few nuclei and large vacuoles, while the pharynx and suckers of the cercaria are composed of cells practically undifferentiated. In the rediae the fibers can be traced to the myoblasts.

The main deep-seated system of muscles for the cercaria consists of the muscle band series of the digestive tract. In the holostome (Fig. 54) an additional muscular activity has been assumed by the cirrus pouch. Aside from these no muscle striae are developed in connection with the genitalia in the larva. The ceca of the digestive tract are covered with an outer and an inner series. The former are longitudinal fibers and the latter are circular fibers. This is in conformity with the muscular layer studies made on other Platyhelminthes.

Histology of the muscle cells. When Bettendorf (1897) showed the connection between the muscle fibers and the myoblasts an important step was made in the knowledge of the intimate structure of the trematode muscle cell. The present study corroborates Bettendorf's work. The nuclei of

the myoblasts are oval (Figs. 118, 119). The cells very early send out long protoplasmic strands along well defined paths. While the processes from the myoblasts may emerge from any part of the cell, the longitudinal strands are always directed in a longitudinal plane, and the circular fibers are always circular. A unique picture is presented at the point where the furcae of the digestive tract arise (Fig. 118). Here there are two anterior processes running cephalad, and three strands proceeding caudad along each cecum. The chromatin in the nucleus of the myoblast is usually confined to the karyosome.

ARMATURE OF THE TREMATODE

The miracidium and sporocysts are not ordinarily provided with hooks or any piercing armature. The redia is usually conspicuous because of its oral sucker, pharynx and gut, and not because of any armature. In the cercaria, however, are found, even in some of the most delicate species, spines covering the basement membrane, especially in the region of the head. In the special group of the stylet cercariae the stylet is the larval organ which is of specific systematic value.

It is not a universal rule, however, that all rediae and sporocysts are unarmed. At times a modification of the posterior wall of the redia is produced as in the redia of *C. biflexa*, where the terminal organ is spinose (Fig. 141). Leiper and Atkinson (1915:202) found the second sporocyst generation of *Schistosoma japonicum* to be covered with a spinous integument. More conspicuous is the prepharynx organ of the redia of *Cercaria pellucida* (Fig. 7). This organ is four-lobed, and has on the outer side of each lobe long spines projecting forward and small spines directed laterad. The use of such a weapon within the soft parts of the host tissue produces untold injury.

No armature has been observed on the body of any monostome cercaria. The holostome, *Tetracotyle pipientis* (Fig. 47), has a spinose covering over the entire body and special spines in the region of the acetabulum and accessory suctorial grooves. Spinose modifications are common in the distome group, and in some cercariae, setiferous modifications of the tail. The types which the writer has examined have the armature confined to the body. They will be discussed under the headings of 1) general body spines, 2) spines of the oral aperture, 3) collar spines of the echinostomes, and 4) the stylet organ of the xiphidiocercariae. In addition there are the spines at the posterior end of the trunk in the caudal pockets. Their probable locomotor function has made it necessary to consider them in another place.

In many cercariae there is a tendency for the entire bodily integument to become modified so that the surface bristles with needle-like spines. These are usually arranged in a regular diamond pattern, and are more fully developed at the anterior end of the body than in the caudal portion (Figure 90). This condition is found in some xiphidiocercariae and some echinostomes. The spines are always pointed forward. They are more fully developed in the anterior region of the body.

Of a somewhat more limited distribution is the oral armature of spines in the schistosomatid *C. gracillima* (Fig. 142). These spines are turned into the body with the inpocketing of the oral sucker-pouch, so that the animal in the condition of contraction appears perfectly aspinose except for the armature of the acetabulum. But with its protrusion the oral sucker is crowned with a solid cap of spines.

The hood of spines of the echinostome group is specialized and valuable in systematic work. It is usually an incomplete ring, consisting of a circlet of spines around the dorsal side, extending ventrad into the middle half of the body. Dietz (1910) has sketched 63 figures of spine characters and numbers in his monograph on the Echinostomidae of birds. The adult echinostomes of North America have received little attention and in consequence of the difficulty in working out the exact spine number in the larva a description of the specific spine characters of the cercariae will not be worth while until more attention is given to the adults of the family.

The stylet is the unique larval organ in the group of the xiphidiocercariae. It might be more properly called a quill than a stylet, for its value as an organ of piercing is questionable on account of its frailty and frequently disadvantageous leverage. It is a mucoid structure, situated in the dorsal wall of the oral pocket, well supplied with muscles to work it in any direction anteriad and laterad. It is fully formed only in the mature cercaria, and is carried into the cyst (Figs. 84, 85). Quite generally the stylet is recognized as of specific systematic value, and is therefore figured in systematic descriptions (Lühe, 1909:189-200), but the stylets as they are figured are so generalized as to be of little value in the identification of species. The stylet is of specific value, but this value lies in the details of the organ rather than in the general outline. (See Figs. 57, 61, 77, 83, 91, 102).

The stylet is usually a weak organ mechanically and poorly levered. However, it is resistent to chemicals and indifferent to dyes. The stylet of *Cercaria glandulosa* is extremely delicate, so that it goes to pieces immediately when a cover glass is pressed down on a water-mount of the worm. The stylet, as a rule, is hard to observe in preserved mounts.

GLANDS OF THE LARVAL TREMATODE

Glandular organs in the trematode may be distinguished as dermal, salivary, mucin, cystogenous, genital, and locomotor. The dermal glands are those imbedded in the subdermal tissues, are unicellular, usually flask-shaped, and have a small duct opening to the exterior. The salivary glands include all of the unicellular glands which open into the digestive tube. Mucin glands are paired, right and left groups of one to several gland cells emptying into the oral pocket thru long attenuate ducts. Since mucin is a constituent of salivary glands, these glands are modified salivary glands. Cystogenous glands are imbedded in the parenchyma and are usually filled with rhabditiform granules which superficially resemble the dermal rhabdites of the Turbellaria but are

not to be confused with them. The cystogenous glands function in the formation of the larval cyst at the time when the transfer to the secondary or definitive host is to be made. Genital glands, in the sense employed here, include only the auxiliary gland elements of the genital system and do not refer to the sex glands themselves. Locomotor glands arise in connection with the locomotor organs in the posterior part of the body.

The dermal glands are of adult significance. Looss (1894:125) has found them in all groups of adult trematodes studied, but he does not later (1896: 219, Fig. 176, *glcu*) record them for any cercariae except *C. vivax* Sons. No dermal glands have been found by the writer in the course of the present study.

Salivary glands are probably present in all groups of cercariae and in some rediae. In the simplest form they are nothing more than pyriform cells in the region of the digestive tube. Thus the monostome cercaria, *C. imbricata*, described by Looss (1896:195) as having a pharynx without a bulb, has unicellular glands massed around the tube in the pharynx region. The furcocercariae, with no true pharynx, have a similar group of cells in the pharynx region, so closely massed together as to lead Looss to considering them a true pharynx (1896:220, Fig. 176, *ph*). In structure these masses of glands in the furcocercariae look superficially like a pharynx (Fig. 142), but on cross-section the cells of the complex are found to be unmistakably glandular (Fig. 152).

A modification of the type of salivary gland just described has been observed in *Cercaria micropharynx*, *C. diaphana*, and *C. glandulosa*. In these species the cercariae show not only the muscular pharynx, but also a large group of gland cells around the digestive tract. In *C. micropharynx* (Fig. 93) the glands are prepharyngeal, grouped in a spherical mass around the oral chamber. They are minute cells, about 3μ in trans-section. The glands of *C. diaphana* (Fig. 76) exhibit a maximum glandular growth in the vicinity of the pharynx proper. Several hundred gland cells about 3μ in diameter surround the pharynx. A case of secretion along the entire digestive tract is found in *C. glandulosa* (Fig. 60). In this species the glands are much larger than in the two preceding species, about 6μ in cross section and 12μ to 25μ in length. They are formed along the entire course of the lumen, from the orifice to the blind end of the ceca, altho they are best developed in the region of the pharynx.

A distinctly different type of gland is that termed the "stylet gland." It is so-named because of its frequent occurrence coincidently with the stylet organ of the xiphidiocercariae. But since it occurs, too, in furcocercariae and in echinostome cercariae, where there is no trace of a stylet, the evidence supports the view that this type of gland is more generalized and more primitive than the stylet organ.

These glands are found in the cercariae of the distome groups examined by the writer, and in the redia of the holostome, *C. flabelliformis*. They are bilaterally symmetrical, lying outside the intestinal furcae, behind the region

of the pharynx. They open thru long-necked ducts into the oral pocket. The glands are in masses; they vary in the number of cells from four in each lateral mass of some furcocercariae (Fig. 144), to eight or ten in the stylet cercariae, while in the echinostomes they run as high as 110 on each side of the esophagus (Fig. 134). In general the cells are characterized by a densely staining granular protoplasm and a highly refractive nucleus, which remains hyaline when treated with hematoxylin dyes. Most interesting is the type presented in *Cercaria crenata* (Fig. 55), where there is a differentiation of inner and outer groups of the glands on each side of the gut. These groups have individual canals to their exit at the oral pocket. The outer series consists of six glands, comparatively small, 8μ to 9μ in diameter, goblet-shaped, extending caudad to the midacetabular region. They are finely granular and are best studied in living mounts. The inner series consists of five cells, two of which are situated just behind the pharynx and the other three postacetabular, thus causing the inner series to be divided into an anterior and a posterior group. These inner gland cells are 11μ to 15μ in diameter, and coarsely granular. Their difference in structure suggests a functional difference.

The mucin glands of the redia of *C. flabelliformis* are paired structures, lateral and dorsal to the digestive pouch, consisting of a single series of six cells which open thru a common tube into the pharynx region of the redia. The cells are similar in structure to the mucin cells of the cercariae of other groups, altho no such glands have been recorded from the cercariae of the holostome group. Only one other case has been reported for the redia, that for the parthenita of *Cercaria equitator* by Ssinitzin (1911:52, Fig. 50). In this redia the gland cells consist of a single cell with a wide duct to the pharynx region. A similar pair of unicellular salivary glands is figured by Looss for the miracidium of *Schistosoma haematobium* (1896, Fig. 113, *glcph*) and by Miyairi and Suzuki for the miracidium of *S. japonicum* (1914, Taf. 2, Figs. 1, 2). This occurrence of the mucin glands in the miracidium, redia, and cercaria of various groups, and the fact that they pass into the intermediate host along with the larva (La Rue, 1917), show that these organs are of fundamental importance in the economy of the worm.

That these glands are of more specific character than the ordinary salivary and epidermal cells of the trematodes is demonstrated by their differential staining reaction. The usual hematoxylin dyes show a great number of granular protein inclusions. Recently La Rue (1917) has shown that these glands in *Cercaria marcianae* have "mucus" in their ducts, because of the staining reaction with toluidin blue and thionin. However, since the glycoprotein of salivary digestion is mucin (Mathews, 1915:323), it is more exact to designate these structures as *mucin glands*.

A type of gland undoubtedly common to all cercariae is the cystogenous gland. It is a unicellular organ in the parenchyma just beneath the integument. In some groups this cell may be small and in the midst of parenchyma cells (*C. glandulosa*, Fig. 62). In other groups the cystogenous cell is very large and conspicuous as in the species *C. pellucida* (Fig. 14), *C. dendritica*

(Fig. 85), and *C. trisolenata* (Fig. 132). The material within the cyst cell is usually milky, semi-opaque, either homogeneous or granular. In most cases the contents consist mainly of the rhabditiform granules, which are indifferent to dyes. These granules are not attacked by weak acids or alkalies, but are digested by strong acids or bases. It seems probable that they are of a derived protein nature.

The formation of the cyst varies in the types studied. In the majority of the species the cyst is a firm envelope with a free space around the embryo, more or less filled with a watery fluid (Figs. 41, 84, 118). On the other hand, some of the cysts are more mucoid in structure, with a granular viscous inner portion and an outer jell (Fig. 11).

The method of encystment differs in different species. In the monostome where the encystment is rapid and an entire lot of mature cercariae encysts in two or three minutes after they are freed from the redia, the process is so rapid that the tail is not entirely cut off until the major portion of the cyst as formed (Figs. 9-11). Where the time of encystment is considerably longer, os in *C. trisolenata* and *C. dendritica*, the tail is discarded long before the process of encystment actually begins. Encystment is an adaptation on the part of the larva to the change in environment. In two cases studied it takes place within the liver of the primary host (*C. micropharynx* and *C. biflexa*). It is highly probable that in these forms encystment was the result of temperature stimuli, since the worms were secured in November when the winter had already set in. It is apparently an adaptation for "wintering over."

In only one group, the furcocercariae, has there been no record of encystment of the cercaria. Here the tail is dropped only under the pressure of the cover slip or when the worm begins to disintegrate. La Valette (1855:34) expresses this condition for his forms when he writes of the larvae: "Cercariae cystibus non indutae in animalium vertebratorum intestinis pereunt."

The phenomenon of encystment is one which has been observed by many investigators. It has been seen and described very accurately by La Valette, Moulinié (1856), Pagenstecher (1857), and a long line of later investigators. Moulinié refers to the studies of earlier workers on encystment, mentioning von Siebold (1835) and Steenstrup (1842). But the credit for the first record of encystment undoubtedly belongs to Nitzsch (1807). Later (1816) this writer records his observations on the encystment of *Cercaria ephemera*. The review of Nitzsch in Isis describes the process of decaudation and encystment as observed by Nitzsch, and shows that this worker expected the cyst to develop the following year. Fantham's criticism of Nitzsch is essentially unjust (1916:12), since Nitzsch considered the cyst to be dormant ands set dead.

The process of encystment has been described in detail by Thomas in his work on *Fasciola hepatica* (1883:129). Encystment here conforms to the rapid type described for the monostome *C. pellucida*. "The tail is sometimes shaken off before encystment begins, but, as a rule, the tail remains in connection with the body during the process, and continues to be energetically

lashed from side to side, until finally a more vigorous movement detaches it. The whole process is very rapid, and in a few minutes a layer of considerable thickness is formed, whilst its substance begins to harden."

EXCRETORY SYSTEM

The excretory system is the most delicate of the four important systems o the trematode. It can be worked out with precision in the living animal, but in preserved material it is impossible to find more than the main trunks of the system. In all of the cercariae and parthenitae described in this paper the excretory systems have been studied from living material. Altho there are many individual differences within groups, yet the fundamental uniformity of groups is evident.

A. The Monostomata. The main features of the excretory system of the Monostomata are the two main trunks arising from a common point just behind the median eye-spot or median pigment center, and proceeding posteriad and laterad to the posterior part of the body, where they join one another in the common vesicle. The bladder opens to the outside thru the excretory pore. which is not terminal but slightly dorsal.

The main excretory trunks are filled with large refractory granules, more extensively described on p. 42. The continuous circuit of the system provides for the transfer of granules and other waste products from right to left and reversely, dependent on the contraction and expansion of the several parts of the animal.

The bladders of the various species differ considerably in size and structure, but as a whole they may be placed in two sub-groups. In the trioculate forms, such as *Cercaria pellucida*, in dorsal view the bladder is distinctly trilateral when relaxed, with the excretory pore at the posterior horn. This same type is found in *C. ephemera* Nitzsch (Ssinitzin, 1905, Fig. 76), and in *C. imbricata* Looss (1896, Fig. 148), and also in *C. zostera* (Ssinitzin 1911, Pl. 1, Figs. 14, 15).

In action, however, due to the muscular movements of the posterior portion of the body, the anterior portion of the bladder may seem to be a separate organ opening into the bulbous posterior portion of the vesicle thru a constricted area. In the binoculate types, on the other hand, the bladder is spherical, with the excretory trunks emptying into the extreme lateral reaches of the vesicle. The excretory pore in these species is subterminal rather than terminal. The only binoculate species known are *C. lophocerca* (de Filippi, 1857, Pl. 1, Fig. 3), *C. urbanensis* (Cort, 1915, Fig. 5), and *C. konadensis*. Lebour (1907:443, Pl. X, Fig. B) describes the bladder of C. *lophocerca* as semilunar, but from her figure it appears more reniform than lunar. Cort does not describe the shape of the bladder of *C. urbanensis*, or state its size. The writer has found it to measure 50μ to 60μ in median sagittal line and 60μ in transverse section for preserved material. The excretory pore of this species is large, some 20μ in diameter; it is weakly muscular (Fig. 35). In *C. konadensis* (Fig. 29) the bladder is small, 14μ to 15μ in diameter. The excretory pore is correspondingly small, 3μ to 4μ in diameter, and weakly muscular.

The excretory system in the tail of monostomes is simple. It consists of a median tubule, with tributary laterals, which swell in the proximal region and empty into the common bladder of the trunk.

B. Holostomata. The excretory systems of Holostomidae and Hemistomidae are sufficiently different to require separate treatment.

1. Holostome type. No accurate or detailed description of the tetracotyle type of excretory system exists. De Filippi (1857, Fig. 26) has pictured two laterals for *C. vesiculosa*, arising from numerous tubules in the anterior part of the body. The connection of these tubes in the region of the bladder is not clear. Altho his sketch was made "to show particularly the lateral vessels," it gives no adequate conception of the fundamental vessels of the system. Brandes (1891:569) merely states that the "system reaches into all parts of the cone; an especially large canal passes longitudinally thru the anterior wall of the cone." Only a faint suggestion of the system is figured by Rosseter (1909, Fig. 17), for *Holostomum excisum* (von Linstow). Brown (1899, Fig. 11) has worked out an interesting but unusual type. In view of the lack of definite data concerning the excretory vessels of the holostomid group, it seems advisable to describe the system for the species *Cercaria flabelliformis*.

The excretory system of *Cercaria flabelliformis* is shown in figure 39. At the extreme posterior end of the worm, situated slightly dorsally, is the excretory pore. It is the opening of a relatively small bladder no larger than the pore itself. At its antero-lateral horns two large trunks arise, considerably inflated in their posterior portion. They may be traced forward along the inner reaches of the digestive ceca until they reach a place about two-fifths the distance from the anterior end of the larva. Here a transverse canal is found, with a median connection between the two trunks, and lateral transverse tubules. The lateral tubules drain the part of the larva posterior and lateral to them. Between them and the main longitudinal trunks are found a great number of anastomoses. Anterior to the median transverse canal the tubules spread out in fan-like arrangement, running to the sides and front of the worm.

Apparently this system was originally distome in character, but was made over to suit the needs of a modified distome larva. The longitudinals are clearly those of the Y-type so common to the excretory system of the distomes. On the other hand, the transverse tubes and the anastomoses of the postero-lateral reaches are new structures.

The entire system is filled with minute refractory granules which facilitate the tracing of the courses of the various vessels.

2. Hemistome type. This type has been worked out in faithful detail both in the larva (Diplostomulum) and in the adult. Hence a discussion of the excretory system of *C. ptychocheilus* will be limited to the points of divergence from the previously described species.

The earliest larvae of this group to be accurately figured are *Diplostomulum clavatum* (Nordmann) and *D. volvens* (Nordmann) (1832, Taf. II-IV). From the elongated bladder there arises a bicornuate structure which proceeds forward and outward for a short distance. A bifurcation of each cornu then

takes place, so that there are two pairs of vessels to proceed forward, an inner and an outer pair. They run forward to a plane in front of the middle of the body, where they unite and run cephalad as a single vessel. A transverse vessel is found posterior to this union; this vessel connects the two sides of the system. Brandes' diagram for the excretory system of *D. abbreviatum* (1891, Taf. 39, Fig. 17) differs from this type only in the details and not in the main features.

The system of *Cercaria ptychocheilus* (Fig. 49) has a long, attenuate non-muscular bladder dorsal to the posterior genital apparatus. It does not pair but gives off a single median longitudinal vessel, which proceeds forward to the midacetabular region, where it gives off the transverse vessel. The median longitudinal trunk then runs forward to the origin of the ceca. Here it gives rise to three antero-lateral vessels. These bend outward and backward, with numerous anastomoses, and finally unite with the lateral traces of the transverse vessel. The outer reaches of the transverse vessel give rise to many anastomoses which are conspicuous in the postero-lateral portion of the body.

The fundamental vessels of the holostome type are the paired laterals and the transverse vessel. Anastomoses and modifications have altered the system appreciably, but not beyond the ability to recognize in them a common type underlying the system, probably reducible to the Y-type of the distomes.

The entire system contains many medium-sized refractory granules which oscillate back and forth thru the vessels at every movement of the animal. By unusual contraction of the worm, the granules are forced into the bladder and out thru the excretory pore.

C. Distomata. The distome cercaria has a simple type of excretory system, consisting of a posterior median bladder with two lateral longitudinal vessels in the body of the cercaria and a median longitudinal vessel in the tail.

1. The xiphidiocercariae. The excretory system of the stylet cercariae consists of a bladder, usually muscular, and a pair of lateral longitudinal vessels which arise from lateral cornua of the bladder. The primitive lateral system consists of three tubules, which emerge from the common lateral soon after the latter leaves the bladder. One of these tubules proceeds posteriad, while the other two run forward as inner and outer tubules. The single median tail vessel ends blindly near the posterior end of the tail; it sometimes receives tributaries, but this is not always the case.

The bladder is a median posterior structure opening to the exterior thru the dorsal pore. It is usually muscular, unpaired. It varies greatly as to size and shape. It may be pyriform (Fig. 90), obovate (Fig. 93), crenate (Figs. 55, 81), truncate or obtruncate (Figs. 60, 100), falciform (Looss, 1896, Fig. 146), or lunar (Looss, 1896, Fig. 179).

The physiological and morphological bladders are not always the same. The former may encroach on the lateral tubules in order to increase its capacity. This may consist of mere enlargements of the cornua without any change in structure (*C. glandulosa*, Fig. 60; *C. micropharynx*, Fig. 90). On the other

hand the needs for a muscular enlargement sometimes cause the muscularization of the cornua (*C. dendritica*, Fig. 81; *C. crenata*, Fig. 55; and *C. racemosa*, Fig. 100). In *C. diaphana* (Fig. 76) the modification of structure has taken place before the enlargement of the long median vessel and the lateral tubes.

The capillaries tributary to the lateral tubules are represented in their most simple form in *C. micropharynx*. The internal anterior vessel may move forward, as in *C. crenata*, or become rudimentary, as in *C. glandulosa*. The external anterior tubule is usually the most fully developed.

It is important to note that the lateral systems of the xiphidiocercariae never anastomose or coalesce in any way. Thus the median sagittal plane acts as a "watershed."

In the forms studied no large flame cells were found in the course of the excretory system. If any minute flame cells were present they were concealed by the thick integument.

The literature shows a paucity of observations on the flame cells of larval and adult distomes. Ssinitzin (1905) shows the details of the flame cells in *Gorgordera pagenstecheri* and in *Phyllodistomum folium*. They consist of an ameboid cytoplasm in which is imbedded a spheroid nucleus with rich chromatic inclusions. This cell is the terminus of the capillary (*cl*). It is ordinarily funnel-shaped, but when distended becomes deeply reniform. The junction of the flame cell and the capillary is marked by a considerable number of cilia which vibrate rythmically, giving rise to Ssinitzin's characterization, "vibratile tip cell of the excretory system."

A detailed study of the flame cell of the adult distome is given by Looss (1896:110; Figs. 72, 77) for *Distomum sanguineum* Sons. The details of the cell *per se* are not appreciably different from those given by Ssinitzin, but the distribution of the flame cells thru the body of the distome is described. There are four symmetrically paired groups of three cells each in the middle of the body, and one pair of two cells each in the anterior and posterior reaches of the body, making sixteen pairs of flame cells and capillaries in all (Fig. 77). This probably gives an indication of the arrangement of the flame cells in the typical distome. In *Distomum isoporum* (Looss, 1894, Fig. 103) six paired groups of ultimate tubules are figured with four flame cells to each group, making forty-eight flame cells in all. In *Distomum cylindraceum* (Fig. 163) there are six paired groups of capillaries with three flame cells to each group, totalling thirty-six flame cells. Thus the number of flame cells is not constant in different species but ordinarily remains constant for each species.

Looss (1894:249, 250; Fig. 186) suggests that the fundamental larval system is the fundamental system of the adult. Extension and modification occur thru a dichotomy of the existing capillaries and flame cells, and an encroachment of the tubules upon the capillaries. The greatest modification takes place during encystment, altho this is in no sense a metamorphosis.

Among adult American distomes the excretory system of *Microphallus opacus* Ward alone has been worked out with the exactitude of the European workers (Wright, 1912, Pl. 17, Figs. 1, 2). This form has the distome

Y-shaped bladder and cornua. There are only eight paired capillaries, and only sixteen flame cells. This condition constitutes a reduction of flame cells from the average types, a reduction which can not be entirely accounted for by the small size of the species.

2. The Echinostome type. This family of distomes is characterized by simplicity of detail in the excretory system except at the head of the main lateral vessel. The bladder is not markedly muscular. The pair of lateral vessels arise from the anterior median region of the bladder, and not from the horns of this vesicle as in the xiphidiocercariae. The main trunks do not divide but proceed to the cephalic extremity along the lateral margins. They sometimes receive small tributaries along their course. In the cephalic region the vessel commonly flexes back on itself. Such flexure may continue back to the posterior extremity of the body, as in *C. reflexae* (Cort, 1915, Fig. 43), or may continue caudad only a short distance, reflexing a second time (*C. biflexa*, Fig. 135). An intermediate form, *C. echinata*, has been described by Looss (1894:191), where the first flexure continues caudad while another part is reflexed cephalad.

A modification of the type represented by *C. biflexa*, where the double flexure is entirely within the cephalic region, is seen in *C. trisolenata* (Fig. 109). Either the end of the flexure has been fused to the most anterior part of the main vessel, or the middle portion of the system has been modified. As a result a triangular channel system has been formed at the anterior end of this excretory system.

The characteristic feature of the excretory system in the two species of echinostomes is the triplet of flame cells at the anterior part of the system. A detailed study of the flame cells in *C. biflexa* is found in figure 138. The cells are situated in the pockets communicating with the ultimate part of the reflexed tubule. Cell *a* is found in the sinus between the secondary and tertiary vessel. It points upward and outward. It is the smallest of the three cells. Cell *c* occupies the swollen end of the tertiary vessel. It is the largest of the three vessels; its cilia are the most rythmical of the group. Cell *b* lies midway between cells *a* and *c*. It points downward and inward. Cells *a* and *b* function in bringing the excretory wastes into the vessel from the surrounding tissue and cell *c* directs the excretory material along the vessel.

The excretory system of certain species of echinostome cercariae contain granules. These granules have been found in all *C. trisolenata* examined; they are found in the lateral vessels from the region of the pharynx posteriad to the acetabulum. They have not been seen in *C. biflexa*.

The excretory system in the tail of echinostome cercariae is not uniform. In *C. trisolenata* there is a single median tube with no prominent tributaries. In *C. biflexa* a median tube runs two-fifths the distance posteriad, where it divides to form two tubules which proceed distad. In *C. trivolvis* and *C. reflexae* (Cort, 1915, Figs. 39, 43) the median vessel of the tail courses backward about one-fifth way and ends there in a bifurcation, the ends of which

open to the sides. The *biflexa* type seems to be intermediate between the echinostome type described by Cort and the more common distome type. It is highly probable that the excretory system of the echinostome, with three flame cells in the anterior portion of the system and possibly several smaller ones further caudad, has arisen from the primitive distome type. In most cases, the posterior flame cells have become fused into larger ones, so that only three flame cells remain in the anterior part of the system in *C. trisolenata* and *C. biflexa.*

3. The Furcocercaria type. The mature apharyngeal distome cercaria of the furcocercous type (i.e. schistosome) has a very small bladder in the posterior part of the body and two lateral vessels running cephalad. The unpaired portion of the tail has a single median canal, which is united to the system of the trunk thru an "eyelet anastomosis." The median tubule of the tail forks to enter the rami. The origin of the caudal vessels has been worked out by Looss (1896, Figs. 172-174) for *C. vivax* Sonsino. These tubules arise as the posterior extension of the paired body excretory tubes. Their fusion in the common portion of the tail occurs after the rami have become well differentiated. The "eyelet" is an index of the original paired system in both body and tail.

A study of the species *C. gracillima* (Fig. 143) and *C. tuberistoma* (Fig. 155) shows the main features of the *vivax* type. The small bladder, the lateral canals, the median caudal tube, bifurcating distally to proceed into the rami, the "eyelet" at the junction of the body and the tail—all of these seem to be constant for the entire group. Beyond these characters the features of the several species are divergent.

In *C. gracillima* (Figs. 143, 145) the caudal portion is extremely simple, containing only the common median tubule and the forked tubule system entering the rami. Unlike *C. vivax* with its three pairs of flame cilia in the common caudal tubule, this species has no flame cells in the caudal portion of the worm. The system in the body of the cercaria has a non-muscular trilateral bladder, small posterior tubes arising from the lateral tubes, and a ciliary pocket about one-fourth way from the posterior margin of the body, on the inner wall of each lateral tube (Fig. 145). At the posterior margin of this ciliary pocket small tributary canals from the median plane flow into the main canal. Slightly cephalad is another pocket, somewhat larger than the ciliary pocket, filled with small granules of various sizes and shapes. Into this pocket four or five small canals empty, the median ones of which anstomose with their mates from the opposite side. No ciliary cells have been found in the terminations of the capillaries.

In *C. tuberistoma* the caudal portion of the worm is characterized by five transverse canals. Another pair, anterior to these, is conspicuous because it runs forward for a short distance and is then reflexed backward for some distance (Fig. 155). The eyelet and the bladder are both muscular. In the body portion there are no pockets for the lodgement of granules and no transverse anastomoses. No flame cells have been found in this larva.

A comparison of the furcocercous larvae with the Schistosomatidae shows the striking similarity of the excretory systems of these forms. Looss (1895) finds the system of male and female *Schistosoma haematobium* alike, altho that of the female may be slightly better developed, due to a minimization of the musculature. The bladder is median, non-muscular, except for a weak sphincter at the pore. It receives the two longitudinals at its antero-lateral reaches. There is no median canal (p. 72). Many of the laterals are dendritic, altho they do not anastomose. Small flame cilia are at the heads of the capillary tubes of 3μ to 4μ diameter. These flame cells and capillaries are intra-cellular, and not surrounded by an epithelial lining.

D. Excretory system of the Parthenitae. Details are given only in observations of Looss (1892:158-161) for the excretory system of young parthenitae. The "protonephridia" of Ssinitzin (1911:77-80; Pl. 1, Figs. 24, 25), described by him in connection with the birthpore of the redia, have not been proved to have an excretory function.

According to Looss the excretory sytem both in the sporocyst and redia arises as a paired structure, from which capillaries and flame cells soon arise. The observations of the writer have been confined to the adult sporocyst and redia of the species studied, in which the system is strikingly different from the embryonic condition. In many cases the excretory system consists of a diamond pattern of intercellular channels, without any clue to the former bilateral symmetry. The same amount of modification holds for both sporocyst and redia. Even in the holostome redia (Fig. 42) this diamond pattern is found. No flame cells have been found in adult parthenitae. This distinct modification of the excretory system in parthenitae is not surprising in view of the extraordinary degeneration of the animal that has resulted from its endoparasitic habits during its entire life.

Excretory granules. The excretory granules of the cercaria and parthenita are spheroidal and have the general appearance of glass beads. Their refractive index is very high. The size of the concretions is variable in different groups and even in the same individual. As a rule the granules are largest in the monostomes and holostomes.

Few writers have given consideration to these excretory granules. Thomas (1883:117) says for *Fasciola hepatica* larvae that "the yellowish granules. . . appear to be excretory products formed within the cells of the sporocyst and then ejected. They are partially soluble in acids, leaving an organic basis." Looss refers to them as opaque concrement-granules which on first sight throw the boundaries of the tubules into black relief (1894:165). They are insoluble in alcohol and color beautifully in stained mounts. Reference is made to these granules by Cort (1915:16) to the effect that the tubules of the monostomes are filled thruout their entire length "with small round concretions which disappear in the process of preservation." The writer has found that these granules are not usually preserved in the corrosive-acetic fixing fluids. However, if fixation is done without the acid fraction of the fluid the granules

are preserved. Application of strong acid to the granule causes an evolution of gas. The granules are negative to inorganic CO_2 tests, and are non-crystalline, as determined by the petrographic microscope. They take hematoxylin stains readily, altho they do not stain deeply. They give no Molisch reaction. The xanthroproteic test is positive, indicating a benzene nucleus. It is probable that they consist of a conjugate protein before fixation. Fixation with mercuric chlorid alters them, since they are then acid and alkali resistent.

Generalizations on the excretory sytem. The excretory system of the trematodes, including both cercariae and parthenitae, is essentially a bilateral system. It arises as two paired tubules, which fuse in the bladder region of the cercaria to form the vesicle. The mature system of the parthenitae is highly modified from the primitive type. The system as found in the cercaria is carried into the adult without very profound modification.

Most individuals of all generations contain within their excretory systems spheroidal concretions, which are waste organic products, quite probably derived proteins. They lodge in the main tubes and are expelled thru the excretory pore.

DIGESTIVE SYSTEM

The most uniform system in the Digenea is the digestive tract. With the exception of the sub-order Gasterostomata and the super-family Prostomata, the enteric canal is triclad in character. The main features of difference in the various families of the group is the modification of the esophagus region of the gut. In most forms there is a pharynx sphincter just within the oral pocket. In other species the pharynx is small and inconspicuous. In still others there is no bulbus around the esophagus, but in its stead a group of gland cells.

The digestive system in the cercaria is not distinctly a larval system but practically a fully matured system. In some cases it is not functional, as in the Monostomata, where the paired ceca are still filled with a jell (Fig. 13); in the Schistosomatidae there is the interesting phenomenon of short ceca in some species (*Cercaria gracillima*) and entire absence in others (*C. tuberistoma*). While the larval digestive glands of the cercaria may not be retained or may be metamorphosed in the mature worm, nevertheless they are functional in most larvae.

The forking of the ceca is not constant, varying in different species. Even the relative length of the parts of the tract varies greatly in the same individual at different times, due to the extreme limits of contraction and expansion of the larva, so that this relation of parts can not be entirely depended on as a basis for diagnosis. As a whole the digestive tract is remarkably uniform and simple, which might be expected in a larva in which the food supply is so accessible.

The sporocyst has no digestive tract, but takes its nourishment directly thru the body wall. In consequence the cells of the epidermis are thin and at times apparently glandular, as in the stylet cercariae.

The redia has a gut-pouch for a digestive system, with a pharynx sphincter around the anterior end. Hence the epidermis is not used in the capacity of food transference, and is heavily lined beneath with an integumentary secretion. For securing food the redia of *Cercaria pellucida* is provided with an oral piercing organ. The redia of *C. flabelliformis* is equipped with paired mucin-salivary glands.

GENITAL SYSTEM

This system of organs has been the most constant basis of classification of adult trematodes. It is also the best specific criterion for the larvae, altho a more delicate technic is required for differentiation of the genital organs in the cercaria than in the adult worm. Because these organs have failed to come out in the ordinary preparations, no attempts have been made to use them as basis for correlating larvae and adults. Cell masses have been figured by Looss (1896), Ssinitzin (1905, 1911) Miyairi and Suzuki (1914) and Cort (1915), but these workers have not in any case shown them in detail. By means of a lengthy staining in a weak solution of Delafield's hematoxylin, followed by rapid differentiation and then neutralization with potassium acetate solutions in the higher alcohols, the genital organs of the cercariae have been traced with a degree of detail not previously attained. These organs have been found to offer valuable data for correlating cercariae and adult trematodes.

A. Monostomata. All three species of monostomes on which observations have been made, *Cercaria pellucida*, *C. konadensis*, and *C. urbanensis* Cort are characterized by the symmetrically arranged testes, the presence of Laurer's canal, the location of the vitelline glands in a double series on each side of the body, and the courses of the uterus and vas deferens. Ssinitzin (1905, Fig. 76) shows the inner series of five paired vitellaria for *C. ephemera* Nitzsch, but he has figured no outer series of three glands, such as are found in the three species worked out by the writer. He is in error in considering them cystogenous glands, because their connection is traceable thru filiform ducts to the ootype. All these species are provisionally referred to the Notocotylidae. With the growth of the cercaria to the adult monostome the originally distinct and readily recognizable vitelline elements becomed fused in part. Looss's figure (1896, Fig. 94) of *Notocotyle verrucosa* (Froel.) shows five rather poorly defined foci of vitelline elements in each of the lateral series. It is possible that the five inner elements of the series have become fused to the three outer elements of the series, thus causing the indefinite outline of the elements in the adult worm. The vitelline glands of *Notocotyle quinqueseriale* are apparently eight to the side. Here the three glands of the outer series may have been introduced between the five glands of the inner series (Barker and Laughlin, 1911, Pl. 1, Fig. 10). A symmetrical pair of vitelline ducts, between the inner and outer series of glands, leads to the ootype.

The cercariae which the writer has studied in this group are readily distinguished by a comparison of their genital systems.

In *Cercaria pellucida* the well-developed cirrus pouch and the poorly developed vagina reach the confines of the excretory trunk just behind the median eye. In *C. konadensis* the cirrus pouch and the vagina are both equally developed. The former is falciform, the later pyriform. The vagina is lateral to the cirrus pouch but is somewhat posterior to it. The genital pore in *C. pellucida* is not as far posterior as that in *C. konadensis*. In this species, as well in *C. urbanensis*, the testes are marked by definite cell masses, while in *C. konadensis* the testicular masses are much more indefinite. They are small in each case and lie ventral to the vitelline organs. The course of the vasa efferentia is clearly outlined.

On the basis of the structure of the vitellaria alone these species can be differentiated in the cercaria stage. In *C. pellucida* the glands are actually spiculate in outline, flattened dorsoventrally. The vitelline material is finely granular and closely massed. In *C. konadensis* the glands are decidedly dendritic, and the granules are diffuse. In *C. urbanensis* the glands are lobate and the fine granules are included within a dense mucoid matrix.

B. Holostomata. The genitalia of the Holostomidae and Hemistomidae will be considered separately.

1. Holostomidae. The thickness of the tetracotyle larva, together with the thickness of the cysts, in which the majority of these individuals have been found, has prevented a study of the genital system from stained toto mounts. However, these organs come out clearly in frontal sections of 7μ thickness (Fig. 39). In *Cercaria flabelliformis* the ovary is situated just caudal to the posteriormost muscular lappet. A short oviduct proceeds dorsad to the ootype. The uterus winds posteriad to the genital pouch. The vitelline glands are long paired cords. In *C. flabelliformis* they are composed of large vesicular glands (Fig. 39); in *Tetracotyle pipientis* (Fig. 47) they are loosely follicular. The testes are paired structures which may occupy positions from the plane of the ovary (*T. pipientis*) to the plane of the genital pouch (*C. flabelliformis*). The pouch is muscular and opens posteriad, ventral to the excretory pore.

Thus these genital organs are typically holostome in character, corresponding to the main features described for the adults by Brandes (1891), Thoss (1897), and Johnston (1904). They are sufficiently detailed in this stage of the species development to be of diagnostic value.

2. Hemistomidae. In this family all of the genital organs are situated entirely posterior to the acetabulum. The primitive genital pore, anterior to the acetabulum, has lost its connection with the genitalia, and with the addition of muscular elements has assumed a suctorial function.

The species *Cercaria ptychocheilus* has an ovary elongate in a transverse plane, nearly spatulate, situated just behind the acetabulum. It is granulate, compact, and stains deeply with hematoxylin dyes. At its left it merges into the oviduct, a large coiled tubule, which bends on itself three times just behind the margin of the ovary, then empties into the ootype just anterior

to the bursa copulatrix. The densely massed cells of the glands in the vicinity of the ootype lie just above this organ. The testes are situated at the right side just ventral to the ovary. They are small compact glands, and have no ducts at this stage of development. The vitelline ducts from the diffuse vitelline follicles meet the other genital products in the ootype. The genital bursa is very large and muscular, and lies just ventral to the excretory bladder. Symmetrically arranged glands, with glandular nuclei and hyaline cytoplasm, empty into it from the postero-lateral reaches. They vary in number from seven to ten on each side.

With the exception of these glands emptying into the bursa, all of the genital organs of this larva lie in the anterior patelliform region. With the exception of the later formation of a uterine duct between the ootype and the bursa, all of the organs are in the approximate location where they will be in the adult worm. The massing of the organs in the anterior portion of the animal is undoubtedly correlated with the abbreviation of the appendicular portion of the species.

The literature on larval hemistomes (Diplostomulum) shows that von Nordmann (1832:34-35, Pl. III, Fig. 1) has described an egg pouch for *D. volvens* and two symmetrically arranged testes, with ducts, in the region of the acetabulum. Leidy (1904:111) describing *D. grande* (Diesing), speaks of "ovaries, dusky yellow." Since the ovary in the Holostomata is single, the organs thus described are possibly testes.

The bursa is the muscular organ *par excellence* in *Cercaria ptychocheilus*. Muscle elements protrude into the atrium, so that a constriction exists between the anterior and posterior portions of the organ.

The genital systems of the holostome and the hemistome are similar in those features in which they differ from the distomes. They have modified their primitive genital pore so that it has either become rudimentary or has assumed a muscular function. The sperm ducts and the uterine duct empty into the pouch at the posterior end of the animal, instead of the atrium anterior to the acetabulum. The new genital pore is posterior to the ootype, and ventral to the excretory pore.

C. Distomata. The genital organs of the distomes are different in various families.

1. Xiphidiocercariae. The genital organs in these cercariae are readily defined with reference to the acetabulum. They are mostly situated in the middle of the ventral side of the larva just behind the acetabulum or slightly posterior to this position. The ootype is posterior and dorsal to the acetabulum. The uterus coils around the right side of the acetabulum. It ends in a blunt or tapering cell mass. Laurer's canal is on the left of the median line, just behind the middle of the acetabulum. It is present in all of the species of stylet cercariae examined. Only in two species are the testicular cell masses outlined. In *C. crenata* (Fig. 59) these glands consist of two large ovate masses.

In *C. dendritica* (Fig. 86) the testes are small, situated closely behind the ootype. In no case is the ovary clearly differentiated from the region of the ootype.

The vitellaria are definitely outlined. These glands in *C. glandulosa* (Fig. 66), *C. diaphana* (Fig. 78), and *C. micropharynx* (Fig. 96) are much more alike than those in the remainder of the stylet species. The vitelline follicles of *C. dendritica* (Fig. 86), and *C. crenata* (Fig. 59) are noticeably dissimilar, having on the one hand, a system extending the entire length of the body, and, on the other hand, a system confined to the immediate vicinity of the ootype.

The genital organs and ducts of *C. racemosa*, the lateral fin type (Fig. 104), bear some resemblance to those of *C. dendritica* (Fig. 86). However, Laurer's canal is very prominent in this fintail species, while in *C. dendritica* it is not so prominent. Instead of coiling around the right side of the acetabulum, the uterus in *C. racemosa* makes four double oblique coils dorsal to the acetabulum. The ovarian cell mass is dorsal to the ootype and connects with that organ thru a short duct. The testes masses have not been observed.

2. Echinostomidae. The two species of this group which have been studied, *C. trisolenata* and *C. biflexa*, vary in the structure of their genital organs most markedly. In view of this diversity it does not seem advisable to take them up in detail in this comparative phase of the study.

3. Furcocercariae. The material of *Cercaria gracillima* was studied with especial reference to the genital cell masses, both in the totos and the section mounts. The main system consists of the ovary-uterus mass on the right and the cirrus mass on the left, both in the vicinity of the acetabulum. The vitellaria are lateral and empty into the ootype thru transverse ducts (Fig. 149). The testicular follicles are numerous, 24 or 25 having been counted. They are proliferated from a posterior germ mass, which is ventral to the bladder

NERVOUS SYSTEM

One of the earlier and better known system of the adult trematode was the nervous system. Leuckart (1863:462) states that Bojanus and Mehlis were familiar with the gross anatomy of the nervous system of the larger flukes, and that von Laurer, Diesing and Siebold as well as the elder van Beneden were acquainted with the nervous systems of both large and small worms. Leuckart described the sytem for *Fasciola hepatica* and *Dicrocoelium lanceatum*. He states that there are two or three stems, the anterior dorsalis and anterior lateralis and the thick posterior ventralis. Somewhat later Lang (1880: 46-50), substantiates the work of Leuckart and, in addition describes the dorsal posterior and acetabular innervation. Gaffron (1884) and Looss (1892, 1894, 1895) have placed the nerve anatomy of the adult trematode on a firm foundation. Hofmann (1899), Wright (1912), and Monticelli (1914) have confirmed the work of earlier workers. Nor has the finer work on the nerve endings and the ganglion cells been overlooked. Many of the earlier writers

made out the ganglion cells of the pharynx region and recorded their observations on the nuclei. Bettendorf (1897), working on *Fasciola hepatica* with intra vitam methylene blue and Golgi methods, has brought out clearly and convincingly the nervous sytem of this worm. This study has been augmented by the work of Zailer (1914).

In view of the extensive study of the nervous system of the adult trematode, it is a matter of no little surprise that so little has been done on the nervous structure of the cercaria and the parthenita. Looss (1894:245) has confessed the difficulty in making such a study and had observed that "ein, wie es scheint, nicht unbeträchtlicher Theil derselben fällt in die Zeit der Cercarienentwicklung, und weiterhin, ist auch der ganze Apparat während seiner Ausbildungzeit, dass es mitunter recht schwer ist, zu entscheiden was zu ihm und was zu dem umgebenden Parenchyme gehört:" However, Looss depended on living mounts for his study and did not use preserved material or avail himself of intra vitam methylene blue technic. By the use of an eosin counterstain against a hematoxylin background the writer has been able to secure remarkably clear sections showing with extraordinary delicacy the nerve branches as well as the central nervous system. It is the purpose of this section of trematode morphology to present data and observations on the development and structure of the nervous system in parthenita and cercaria.

The central nervous system of the adult trematode consists of two central ganglion masses, situated dorsal and lateral to the pharynx and yoked together by a transverse commissure passing dorsal to the pharynx. The appearance of this structure has been aptly described by Lang (1880:46) as a saddle between oral sucker and pharynx. In cross section it is lunar. Here are centered the most of the ganglion cells, altho they are frequently found posteriorly, and often in the sensory apparatus of the oral and ventral suckers. The system also has a subesophageal commissure which differs in size and shape in different species of flukes. Extending forward into the region of the oral sucker are three pairs of nerve trunks, the dorsalis, lateralis, and ventralis. Of these three the latter is the most fully developed. It has a ramus muscularis which is both motor and sensory (Zailer), and an extensive connection with the oral nerve ring. The anterior lateralis is also a strongly developed trunk, with a ramus muscularis and a ramus palpalis, and transverse commissures to the anterior dorsalis and posterior lateralis. The anterior dorsalis is a weakly developed nerve which innervates the apical sensory field. A transverse commissure connects the two dorsales above the head muscle sheath. In addition to these three primary trunks, the palatinus, a weak motor nerve, lies internal to the anterior ventralis. Posterior to the central nervous system are the three posterior trunks, the dorsalis, lateralis, and ventralis. The ventral trunk is by far the most strongly developed. In addition to these is the small but conspicuous internal branch of the ventralis known as the pharyngealis. It occupies a posterior position, corresponding to the palatinus anterior to the central nervous system.

Braun (1893:683) considers the ventralis, dorsalis, and pharyngealis to be the three pairs of posterior nerves. However, the consistent course of the lateralis to the posterior extremity of the body, its early appearance in the embryology of the worm, and its commissural connections with the anterior lateralis and posterior dorsalis surely prove its right to a place in the rank of the primary posterior nerve trunks.

The nervous system of the monostomes has been worked out by Jägerskiöld (1891) for *Ogmogaster plicatus* (Crepl.), and by Monticelli and Looss for *Catatropis verrucosa* (Fröl.). Looss (1896:149) considers the system similar to the distome type. "Je n'hésité pas à attribuer au système nerveux de notre ver une construction analogue a celle que nous avons déjà signalée chez un bon nombre de Trématodes digénèses." However, Looss (1896:11-16) was not able to make out clearly the anterior trunks. Jägerskiöld (1891:14-16) describes the cerebral ganglion masses with the transverse commissure, the posterior ventralis, dorsalis, and lateralis, and the three anterior trunks, short and thorn-like, the homologs of the dorsalis, lateralis, and ventralis. A stem, designated as the "fourth," arising from the anterior reaches of the cerebral masses, passes ventrad to the region below the oral sucker; it seems probable that it is the palatinus. The only real modification from the distome type is the absence of the acetabular innervation, due to the loss of this organ.

In the Amphistomata adults among the earlier writers Lejtenyi (1881:142-144), working on *Gastrodiscus polymastos* Leuck., described two ganglion centra with the dorsal commissural bridge, but with only one anterior and one posterior pair of trunks. In contrast to this incomplete description is that given by Looss (1896:21, 22) for *Gastrodiscus aegyptiacus* (Cobb), where the usual distome nerve trunks were found, and, in addition, a median anterior and a median posterior nerve. Looss has worked out the nerve anatomy for *Amphistomum subclavatum* Rud. in even greater detail (1892:151; Taf. 19, Figs. 1, 2,), and finds that they correspond to the distome type, except for the innervation of the posterior sucker.

The one group of the Digenea where the nervous system has been almost entirely neglected is the Holostomata. Brandes (1891) states that none of the workers of the nervous system up to his day have worked on the holostomids. He has observed only the central nerve center lying above the posterior portion of the pharynx, an anterior and a posterior pair of nerve trunks, the tracings of which he has found in sections. Thoss (1897), working on *Holostomum cucullus*, finds the main nerve center lying dorsal to the origin of the esophagus, with two pairs of anterior and one pair of posterior nerve trunks.

The central nervous system of *Cercaria trisolenata*, the echinostome, consists of two masses of ganglion cells and the dorsal commissure lying concavely on the dorsal side of the large muscular pharynx. The commissure is broad and flat. The dorsal surface of the ganglion masses and the commissure present a smoothly curved surface, but on the ventral side the ganglia bulge out against the pharynx. The anterior trunks consist of the dorsalis, lateralis, ventralis, and the palatinus. The paired dorsales arise together with the

laterales and proceed forward with them for some distance. After separation, the dorsalis runs more median, then flexes outward and dorsalward over the oral hood, proceeding toward the apical sensory center. The lateralis at the point where it leaves the dorsalis proceeds outward and forward, so that it reaches a level slightly below the plane of the central nervous system. Slightly after diverging from the dorsalis the lateralis gives back a commissure to the dorsalis. This dorsolateral connective fuses with the dorsalis just behind the posteriormost branching of this trunk. Arising from the most ventral reaches of the ganglion center is the ventralis, a broad flat trunk, which courses outward and downward to the oral lip of the oral sucker. Internally it gives off the palatine, which lies just lateral to the pharynx.

Caudal to the central nervous system arise the four pairs of posterior trunks, the dorsales, the laterales, the ventrales, and the pharyngeales. The dorsalis branch arises dorsal and slightly lateral to the junction of the ganglion and the commissure. It runs straight backward, slightly dorsal to the plane of the central nervous system. The lateralis arises slightly lateral to the dorsalis; its path lies outward and backward. The ventralis arises from the very heart of the ganglion mass. It spreads outward and then runs backward parallel to its mate. The ventral commissure, arises just median to the origin of the posterior ventralis flexing below the prepharyngeal opening. It is stout and bowed considerably downward. Between the commissure and the ventralis arises the pharyngealis.

In a germ ball of *Cercaria trisolenata* some 45μ by 60μ in size, the central nervous system is well developed. This may be called the *butterfly stage* (Fig. 121). At this period there are two pairs of main trunks anterior and four pairs posterior to the central ganglion mass. The anterior trunks are the ventrales and the laterales. By reference to the next stage in the development (Fig. 122), the dorsales are found to arise from the sinus between the laterales buds of figure 121. They arise at first as a single bud and bifurcate later. Caudally the most conspicuous trunks are the dorsales, which arise in a median plane and conspicuously dorsal to the other posterior trunks. The dorsal commissure at this period is practically negligible. The outermost ventral trunk-buds are the laterales, short and stubby at this period of growth. The ventral trunks arise from the ventral portion of the cerebral masses. Between them and the laterales arise trunks which are present in the embryonic stage only. They may be designated as the posterior intermedius nerves.

In stage II (Fig. 122) a very decided change has occurred in the outline of the central nervous system, altho the fundaments of the first stage described are present. Anteriorly the intermediate space between the laterales has disappeared and from that region has arisen a wedge which is the fundament of the paired dorsales. The ventral trunks have been set off to themselves by a lateral growth and elongation of the intermediate fibers. On the caudal side of the ganglion the posterior dorsalis has been separated from its mate by the growth of the dorsal saddle commissure. Most noticeable, however, is the

change that has taken place in the ventral portion of the system. Here the space between the ventrales has become exceptionally wide and a prominent commissure has grown out from the trunks, commonly known as the subesophageal commissure. It is the homolog of the transverse commissure occuring along the entire ventral side. The intermedius trunk has become fused with the posterior lateralis, in part, and then crosses over to the ventralis. This is the connection known in adult nerve anatomy as the ventrolateral commissure, a strong and important intercommunicating trunk (Fig. 123). In the developmental stages no trace of palatinus or pharyngealis has been found.

Cercaria glandulosa, a xiphidiocercaria, is favorable material for the study of the minute structure of the nerve fibers and endings. In the anterior end of this larva there occur in five frontal sections of 8μ thickness all of the fundamental nerve endings of this region. In section 1 of the worm (the most dorsal section), there are no nerve structures save a few sensillae to the dorsal lip of the oral sucker. They receive innervation from the anterior dorsalis, and derive that innervation from the anteriormost fibers seen beneath in section 2, just in front of the musculus preoralis. Section 2 (Fig. 68) shows the trunk of the dorsalis descending into the oral musculature. It has three main branches, one coursing to the preoral region to supply the conductive strands for the preoral sensory endings, one becoming the short superficalis, and a longer one, the profundus, passing under the endings of the superficialis. In the region of the musculus preoralis, the apical sensory field is continuous across the sucker from right to left. In section 3 (Fig. 69) are illustrated the main outlines of the central nervous sytem, together with the anterior trunks. Here is the dorsal portion of the ganglion cells. Anterior and dorsal is the dorsal commissure and ventral is the subesophageal commissure. The forward traces are the trunks of the laterales with the outermost superficial ramus palpalis and the more deeply situated ramus muscularis. The latter branch innervates the musculus preoralis and the anterior lip of the oral sucker. On the left is the trunk of the anterior ventralis, arising from below the mass of the ganglion cells. At the anterior extremity is the apical sensory field. The dorsolateral commissure is very clearly shown in this section. Section 4 (Fig. 70) shows the remainder of the central ganglia with the left anterior ventralis passing forward. This is a large trunk, with an especially important ramus palpalis leading to the apical sensory field, and a small oral nervus communicans supplying the oral nerve ring. This ring completely encircles the superficial region of the oral sucker and connects with the superficial branch of the dorsalis. The ramus muscularis of the ventralis and the palatine branch of the ventralis are found in section 5 (not figured).

Passing caudad all the posterior roots are well defined. Four posterior roots are visible in section 3 (Fig. 69). These include the posterior dorsales, laterales, ventrales, and pharyngeales. In a fortunately cut section of the same species the innervation of the acetabulum is beautifully demonstrated (Fig. 71). The two main longitudinal trunks, the ventrales and the laterales,

are connected by commissures. Those around the acetabulum are of especial importance. The preacetabular commissure arises from the lateral trunk and proceeds in a posterior oblique course, then around the anterior reach of the acetabulum to meet the branch from the other side. The postacetabular branch arises from the lateralis also, but continues caudad along the course of the ventralis. Behind the acetabulum it meets the branch from the opposite side to form the span. From these trunks circumscribing the acetabulum two ring commissures arise, a superficialis and a profundus, of which the latter with the nerve endings is found in the section (Fig. 71).

The nervous system of the monostome, as worked out by Jägerskiöld (1891, Taf. I) for *Ogmogaster plicatus* (Crepl.), has been substantiated for the most part in the study of *Cercaria pellucida* (see figure 23). The three paired posterior trunks are evident. The posterior ventralis is the most important of these and can be traced to the caudal extremity of the animal in all cercariae of this species, as well as in *C. konadensis* and *C. urbanensis*. The dorsalis is less conspicuous, yet it is usually traceable far caudad. The posterior lateralis is delicate. It arises near the origin of the ventralis and swings out laterad in a great bow. It, too, can usually be traced to the posterior extremity of the body.

The anterior trunks can also be definitely traced. The ventralis arises from the extreme lateral horn of the ganglion center in conjunction with the posterior ventralis. More median, the anterior lateralis is found. The two anterior dorsales arise as a single structure along the median line. Their primary function in the cercaria is the innervation of the median pigment eye, altho branches may be traced farther anteriad. Likewise, an important branch of each posterior dorsalis constitutes the nerve tract to the lateral eye.

The ganglion cells in the monostomes are superficial to the nerve strands. A considerable number of them are not even in intimate contact with the fibers, but have fibrillar communications with them. The ganglion masses from which the nerves arise are distinctly cornuate, with a wide dorsal commissure.

Pigmentation and eye-spots in the monostomes. The monostome cercariae that have come under the direct observation of the writer, together with those described in the literature, may be placed in two groups according to their eye-spots, namely, those with a single pair of eye-spots, disposed laterally to the brain center, and those with an additional median eye, anterior to the central nervous system. The amount of pigmentation is considerably larger in the trioculate species than in the binoculate type. Figures 1 to 3 show in dorsal view a series of stages in the pigmentation of *Cercaria pellucida*. The pigment originates anteriorly over the brain center and proceeds caudad along six lines of growth. A very careful study of the pigmentation in these species indicates that a very simple but reasonable relation exists between the pigmentation and the underlying nervous system. The pigmentation is found to be a delicate superficial index of the underlying nerve fibers. This

pigmentation is present in the subintegumentary areas and follows with precision all the ramifications even to the nerve endings. Figure 37 shows the nerve endings in the anterolateral reaches of *Cercaria pellucida*.

In the paired eye-spot a definite subspherical "lens" is found in the region of the concentration of the pigment. In the median eye of the trioculate type a "lens" is sometimes present. The origin of the eye is simple. At an early stage in the germ ball (60 μ to 80 μ), when the cell masses of the nerve trunks are definitely outlined as they emerge from the ganglion center (Fig. 36), a branch of the posterior dorsalis, larger than any other nerve, pushes out obliquely. It meets an invagination of the ectodermal layer, which may be considered an "optic cup." There soon forms in the hollow of the cup a group of dark brown refractory granules, which entirely lines the optic cup several layers deep and leave but a small cavity within. The optic branch of the dorsalis bends back into the cavity at the place where it first comes in contact with the cup and here ends in a pyriform enlargement, the nerve cell. The structure of this end organ is such that it might be interpreted as a "lens," if the connection with the nerve is not made out. Cort (1915:15) has placed that sort of an interpretation on the eye structure of *C. urbanensis* and *C. inhabilis*. For the former he states that "each true eye is formed by a mass of pigment in the form of a cup, the bottom of which is thicker than the sides. A lens fits into the opening of the cup, leaving a space between its lower surface and the bottom of the cup." And again, for *C. inhabilis*, "the large eyespots . . . are composed of the lens and the cone of pigment like those already described for the monostome, *Cercaria urbanensis*." The writer has studied some of Cort's material and has found sections where such an interpretation might be made from a single section. But in the preceding or following section the connection of this "lens" with the optic nerve is plainly seen.

The eye structure as studied in this monostome is similar to that found in the Monogenea, especially the type in the posterior eye of *Tristomum molae* (Hesse, 1897:559; Taf. 28, Fig. 29).

The nervous system of the monogenetic trematode was first studied in detail by Lang (1880), who made out the pigment cup, a refractory body (lichtbrechender Körper), a ganglion cell, the retina, and eye muscles (p. 41; Taf. I, Fig. 2, Taf. II, Fig. 2). Most later investigators mention only the perceptory body and the accessory apparatus, altho André (1910:217) has identified the muscle fibers of Lang. The writer believes that the movement of the eyes depends largely on the general bodily movement.

In the adult Monogenea studied the pigment cup is found to lie between the refractory bulb of the eye and the possible source of light (Goto, 1894:81). In the monostomes, as in *Dendrocoelium lacteum* (Hesse, 1897, Taf. 27, Fig. 10), the hollow of the cup is directed outward, so that light falling on the eye must pass thru the end organ before reaching the inner portion of the pigment complex.

The pigment of the organism is probably the waste product in the metabolic economy of the worm. Its close association with the nerve endings in the

monostome cercariae seems to indicate that it is the melanoidin fraction of the oxidative processes in the nervous system. The possibility of utility as a receptor of light or heat is a secondary item and must not be confused with the primary meaning of the pigmentation.

In the free-living Platyhelminthes the fully developed eye is present in the mature individual. In the ectoparasitic trematodes the eye-spot is well developed in the young animal (Hesse, 1897:560, 561), but degeneration takes place as the animal matures. Goto (1894:81), speaking of Tristomum, observes: "Morphologically speaking they are certainly degenerate eyes; and have probably been derived from such eyes as are found in Turbellaria; but I do not think they are functional. In the first place the pigment granules are situated on the dorsal side and thus prevent the light from reaching the lens, since the dorsal side is the only direction from which light can come. In the second place there is not always a distinct retina. If these 'eyes' are really still useful to the animal, they may possibly be a temperature sense organ; and for that purpose their structure seems to answer well." Goto goes on to show that the more degenerate condition of the eyes in *Tristomum ovale* is due to the greater degree of internal parasitism of this species than that of *Tristomum molae*. In the monostome, the eyes are well developed in the cercaria but become fully degenerate, with a loss of all the pigment in the adult, so that the adult of one species has been described by Creplin as "albidus" (Jägerskiöld, 1891:4). In some species of Allocreadiidae (*Crepidostomum farionis* O. F. M. and *C. cornutum* (Osborn)), pigment eye-spots are found in the adult. A still further stage of degeneracy is found in *Cercaria racemosa* (Fig. 100) and *C. gracillima* (Fig. 144), where the optic nerve is still present but the pigmentation is absent.

In *Cercaria gracillima*, the representative of the furcocercariae, the nervous system is narrow, in correspondence with the attenuate condition of the animal. The posterior laterales are not found in the mature cercariae, altho the bud is present in the germ ball (Fig. 151). One is struck by the significant resemblance of the main nerve complex of this cercaria and that of *Schistosoma haematobium*, described in detail by Looss (1895). The three pairs of anterior trunks are readily made out, altho, in addition, a prominent dorsolateralis is found (Fig. 150). The posterior dorsalis arises from the dorsal side of the ganglion cell mass and proceeds caudad to the region of the acetabulum, where it fuses with the ventral trunk. A prominent subesophageal commissure and a small pharyngealis are present. The fundamental resemblance between the system described for this cercaria and that for the schistosome adult seems to the writer to be sufficient morphological evidence for the correlation of these apharyngeal furcocercariae with the Schistosomatidae.

A study of the nervous system of the Holostomata has been made of *Cercaria ptychocheilus*, based on both toto mounts and sections (Fig. 53). No adequate idea of the nervous system of this group can be secured from the meager data of Brandes (1891) and Thoss (1897). The dorsal commissure is

indistinct and thoroly fused with the ganglion masses. The latter are wide, with a construction in each in the region of the origin of the lateral trunks. The trunks figured by Thoss are probably the ventrales, since they supply the main innervation of the animal. The anterior ventralis arises along with the posterior ventralis just anterior to the latter. The anterior trunk soon divides. The major portion runs around the oral sucker, while the external branch is traceable anterolaterad. The anterior lateralis is represented by a blunt stock just outside the pharynx. It runs cephalad but soon ends in two delicate branches. There is no posterior dorsal of posterior lateral. The posterior ventral is stout and thick. It gives off one prominent branch externally soon after it reaches its most external position. At regular intervals it gives off branches internally which have the indication of rudiments of commissures. These transverse trunks just anterior and posterior to the acetabulum are still well developed; they are similar to those described for the distome.

Contrary to the opinion of Looss (1894:245, 246), the writer has found without exception that the general trematode nerve anatomy can be traced from the early germ balls up thru various stages of growth, and that the cercaria shows not only the potentialities of the adult system, but actually the details of this system. Moreover, the study of various groups of cercariae has demonstrated that the fundamental deviations and modifications from type are recognizable in the mature cercaria. Thus this study has shown that the nervous system of the cercaria is constant for the group to which it belongs, and is a definite basis for the natural classification of the groups.

In contrast to the highly developed nervous system found in the cercaria is that of the parthenita. In the sporocyst no definite nerve complex is found, altho Looss (1892) has observed nerve elements in miracidia of *Amphistomum subclavatum*. In the redia, however, with the continued functioning of the highly muscular pharynx, there is a nerve complex practically embracing the entire anterior portion of the gut (Fig. 125). Viewed from the dorsal, ventral, or lateral aspect, the system in surface view appears as an H. It is resolvable into four anterior trunks, four posterior trunks, and a ring commissure. On the dorsal side are two swellings, the rudiments of the cerebral ganglion masses of the cercaria. The nerve cells of the system are very prominent. They are usually bipolar or multipolar (Fig. 126), but, as might be expected, the more superficial ones are more often the multipolar cells.

This redia nervous system constitutes a very primitive type, in which the nerve cells are much more frequently diffuse and more discrete than in the systems in the cercariae. It is probable that the pharynx is responsible for keeping the system from total degeneration.

The size, number, and location of the ganglion cells vary according to individual species of cercariae. They may be situated within the ganglion centers, as in *Cercaria micropharynx* (Fig. 97) and *C. glandulosa* (Figs. 69, 70); they

may be scattered around the ganglia altho not imbedded in the fibers. In the redia of *C. trisolenata* the fibers are less conspicuous than the ganglion cells. Species closely related may have cells of different numbers and different sizes. In *C. micropharynx* there are always just two ganglion cells, imbedded in the fibers, just above the esophagus. Their nuclei are large, pyriform, and usually containing conspicuous refractory nucleoli. They measure 5.5μ to 6μ in short diameter by 8.5μ to 9μ in long diameter. The nucleoli are about 2μ in diameter. *Cercaria glandulosa* presents a case where there is a definite number of minute ganglion cells within the ganglion masses. There are fifteen cells in each of the two masses. The cell walls are not well defined, but the nuclei are readily distinguished. They measure 1μ to 1.5μ in short diameter by 1.5μ to 2μ in long diameter. The ganglion cells of *C. pellucida* are numerous; it has not been ascertained whether they are constant in number. They are subspherical at times, but are usually multipolar. The entire cell averages 3.3μ by 6μ while the nuclei measure 1μ to 1.6μ. The cells of the redia of C. *trisolenata* are usually multipolar in the region of the epidermis. They range from 6μ to 22μ in diameter. The nuclei are inconstant in size, varying from 2μ to 6μ in diameter. The nuclei of the ganglion cells of *C. gracillima* are so minute in the nerve complex in the germ balls (Fig. 151) that they are barely visible under 1,000 magnification. Yet these nuclei are definitely set off from the surrounding matrix. They measure about 0.4μ in diameter.

In cell-studies of adult trematodes the nerve cells have been measured in many cases. The measurements range from 80μ (Lejtenyi, 1881:41) in *Gastrodiscus polymastos* to 6μ (Fischer, 1883:17) in *Opisthotrema cochleare*. The nuclei range from 12μ (Juel, 1889:41) in *Hemiurus excisus* to 1.6μ in *Opisthotrema cochleare* (Fisher). A comparison of these measurements in adult trematodes with those for the cercariae, shows that the nuclei of the adult cercariae are as large as those of the adult trematode. It is evident, however, that the cells are much smaller in the cercariae. Ageing of these cells consists, then, in the growth of the cytoplasm rather than an increase in size of the nucleus.

DESCRIPTION OF THE TREMATODES INFECTING MOLLUSKS OF THE BITTER ROOT VALLEY

INTRODUCTION

On account of the biological isolation of the Bitter Root Valley, it is little wonder that it contributes new species of trematodes. The fourteen species of trematodes found in the valley are not thot to comprise the entire trematode fauna of the region, but are the representative species for the year and season when the study was made. Of the fourteen species found in the Bitter Root River, two are larval Monostomata, two are Holostomata, and the remaining ten are Distomata. In addition to these, a larval holostome, *Tetracotyle pipientis* nov. spec., from the vicinity of Chicago, Illinois, is included in the study for the sake of comparison.

Previous to the writers' preliminary report (Faust 1917) the following larval trematodes have been described for North America.

MONOSTOMATA

Cercaria hyalocauda Haldemann 1842
Glenocercaria lucania Leidy 1877
Cercaria urbanensis Cort 1914

AMPHISTOMATA

Cercaria inhabilis Cort 1914
Cercaria diastropha Cort 1914
Cercaria gorgonocephala Ward 1916

DISTOMATA

Cercaria agilis Leidy 1858
Rhopalocerca tardigrada Leidy 1858
Gymnocephala ascoidea Leidy 1877
Cercaria platyura Leidy 1890
Cercaria reflexae Cort 1914
Cercaria megalura Cort 1914
Cercaria leptacantha Cort 1914
Cercaria caryi Cort 1914
Cercaria isocotylea Cort 1914
Cercaria brevicaeca Cort 1914

DISTOMATA

Cercaria polyadena Cort 1914
Cercaria hemilophura Cort 1914
Cercaria trigonura Cort 1914
Cercaria trivolvis Cort 1914
Cercaria rubra Cort 1914
Cercaria douthitti Cort 1914
Cercaria wrightii Ward 1916
Cercaria anchoroides Ward 1916
Cercaria marcianae La Rue 1917 (Really a *Distomulum*)
Cercaria vergrandis La Rue 1917 (Really a *Distomulum*)

HOLOSTOMATA

Diplostomulum cuticula (v. Nordmann 1832)
Diplostomulum grande (Diesing 1850)
Diplostomulum volvens (v. Nordmann 1832)
Tetracotyle typica (Diesing 1858)
Diplostomulum parvulum (Stafford 1904)

Cercariaeum

Cercariaeum helicis (Leidy 1847) Later recorded by Leidy as *C. vagans* (1850).
In addition, there is the doubtful form, *Cercaria bilineata* Haldemann 1840.

According to Stiles and Hassall (1908:157), Leidy is credited with the record of a species, *Diplostomulum rhachiaeum* (Henle). Investigation of the literature shows this to be an error, owing to the confusion of the names Leidy and Leydig. Fr. Leydig described the species *D. rhachiaeum* for Europe in 1853 (Leydig, 1853:383).

Of the thirty-two forms listed, it is doubtful if any except those described by Cort (1914), Ward (1916) and LaRue (1917) could be recognized by their descriptions, since in the majority of cases the data are so indefinite as to leave the systematist a wide range of choice in determining the species. An excellent

example of this valueless type of description is afforded in the form *Diplostomulum cuticula* (von Nordmann 1832), reported by four American investigators from various localities east of the Rocky Mountains. The descriptions include larvae encysted with pigment and without it, some specimens found subdermally, others taken from the peritoneum of the body cavity, all secured from a great variety of teleost fishes. In none of the descriptions is there mention of the course of the excretory system or of the genital cell masses, both of which are essential to the exact determination of the species. It seems reasonably certain that a careful revision of these forms described as *Diplostomulum cuticula* (von Nordmann) would result in the discovery of several new species of Diplostomulum.

The species of cercariae and parthenitae described in this section of the paper have been studied with special reference to the excretory, genital, and nervous systems.

MONOSTOMATA

Cercaria pellucida Faust 1917

This larval trematode is a muscular cercaria, characterized by heavy anterior pigmentation on the dorsal surface, centered around three foci, the paired lateral eye-spots and the median eye. It is a member of the trioculate group of the Monostomata. The pigmentation tends to spread caudad from the pigment center along six lines of growth, two dorsal, two lateral and two ventral. These lines of pigment have been shown (p. 53) to be the superficial index of the underlying nerve trunks. The worm is characterized by 1) a transparent body, 2) a circuit of refractory granules that marks the excretory system, 3) a small oral sucker, and 4) large longitudinal muscle bundles of the tail.

Cercaria pellucida was obtained from *Lymnaea proxima* Lea in the Bitter Root River in the vicinity of Corvallis, Montana, and from *Physa gyrina* Say near Buckhouse Bridge. The snails were examined in October, 1916. *Lymnaea proxima* contained a heavy infection with this species, along with a lesser infection with the monostome cercaria, *C. konadensis*, and a distome larva, *C. diaphana*. Physa was heavily infected with an echinostome, *C. trisolenata*, and contained only a light infection with the monostome. In all cases the infected organs were the liver ceca.

The mature *C. pellucida* has an average measurement of 0.4 mm. to 0.7 mm. in length and 0.18 mm. to 0.2 mm. in width. The tail is about 0.5 mm. long and has a diameter of 0.07 mm. at the base. Most usually the animal has an elliptical constricted outline, such as is shown in figure 4, but when relaxed it assumes the elongate-ovoid or spatulate condition, shown in figures 1 to 3.

The parthenita is a large conspicuous redia, measuring 2.2 mm. by 0.5 mm. (Fig. 6). Within the redia is a large rhabdocoel gut extending almost the entire length of the animal and measuring 0.3 mm. in cross section. The gut empties anteriad thru a muscular bulbus 15μ in length and 12μ in cross sec-

tion. It is spinose internally (Fig. 20). In the prepharynx region is a unique piercing organ (Fig. 17), probably of ectodermal origin. It is four-lobed and is covered with spines. A rythmic eversion of the organ against the host tissue and redrawal within the pharynx region of the parthenita is a characteristic movement of the redia. Around the muscular pharynx is a ganglion mass consisting of a fibrous matrix and a network of ganglion cells. Behind the head region is a neck-like constriction, and behind the neck is a sacculate body. At the extreme posterior end is a large papilla. The redia is covered with a non-cellular basement membrane, and imbedded in this superficially in the form of minute tuberosities are the remains of the epidermal nuclei (Fig. 22).

The walls of the redia are well-supplied with muscular layers, longitudinal and transverse, so that the parthenita is capable of extraordinary distension and contraction, altho it has no specific locomotor organs.

The germ balls of the redia arise from the matured ova, derived from four cells localized at the posterior extremity of the parthenita. Altho the cells lying next to the wall around this quartet may be potentially germ cells, they take no part in the ordinary proliferation of germ cells (Fig. 22). From these cells arise the germ balls, thru cleavage into 2, 3 and 5 cells, after which certain cells of the ball appear much smaller than the others and grow over the latter, giving rise to the gastrula by epiboly. The young germ balls usually lie en masse behind the gut, while the more advanced cercariae are crowded anteriorly. They appear strangely grotesque, with their pigment eyes and their snout-like bodies oscillating back and forth within the body wall of the parthenita.

Aside from the larger size of the body and the trioculate anterior end, *Cercaria pellucida* might be at first confused with *Cercaria urbanensis* Cort. While the size and eye-spots are sufficient to separate these two species, a more careful examination shows that there has not been a separation of two species at all, but more correctly two groups of species. The group of smaller species is binoculate and ranges around 0.3 mm. to 0.46 mm. in length by 0.1 mm. to 0.16 mm. in width, while the group of larger species is trioculate and averages around 0.5 mm. in length by 0.15 mm. to 0.2 mm. in width. Consequently from a description of external characters alone there is no means of separating *Glenocercaria lucania* Leidy from the Bitter Root species *Cercaria pellucida*. It is such a problem as this that has caused the writer to believe that there are characters more deeply seated in the larva that will readily set it off from others of the same group.

Sufficient care in technic makes it possible to bring out very clearly and convincingly the genital organs of the Bitter Root species. Here are characters, constant both in the larva and the adult that readily differentiate these monostome cercariae. These have been described in detail in the section devoted to morphology (p. 45) and need only to be summarized at this point. The median ovary just in front of the excretory bladder opens out thru a short duct at its left (Fig. 18), and after receiving the common vitelline duct, opens

anteriad into the uterus. This organ has an outlet just behind the median eye. It ends in a poorly developed vagina. No Laurer's canal has been definitely made out in the totos but there is evidence of such an organ in sections. From the sides and slightly caudad to the ovary the closely massed testes open into filiform vasa efferentia which unite anterior to the ovary to form the vas deferens. This canal is directed forward parallel to the uterus, ending in a bulbous cirrus pouch just to the left of the vagina. The three paired outer vitelline follicular masses and the five paired inner masses occupy a dorsal position. They are irregular in contour (Fig. 4), with aciculate margins, and are finely granular with close massing of the granules. Inconspicuous common vitelline ducts connect the vitellaria with the ootype just dorsal to the ovary.

The excretory trunks are similar to those of the entire group of monostomes. The bladder is quite small, 48μ in section, moderately muscular, superficially triangular, with the excretory pore posterior. The excretory tube in the tail is vesicular at the base and narrows down distad (Fig. 4). The tubes of the trunk are crowded with large excretory granules.

The digestive system is typically triclad, with ceca extending to the subdistal extremity. They are filled with a jell, and are crowded with granules imbedded in the jell. No pharynx has been observed. The oral sucker is directed ventrad. It is small but powerful.

The parenchyma is filled with cystogenous granules, included in one-celled cystogenous glands, probably of mesodermal origin (Fig. 14). Between the cystogenous cells are angular parenchyma cells, more commonly known as vesicular cells (Blasenzellen), with processes extending to the integument and possibly functioning in the capacity of secretory ducts for the basement membrane.

The locomotor organs at the posterior angles of the trunk are neither spiculate nor spinose. They possess no cement glands. The tail has no central pair of gland elements such as are found in binoculate cercariae of the monostome group. However, the ordinary parenchyma cells of the tail of *C. pellucida* are remarkably large and vesicular and suggest a glandular function (Fig. 19.).

Large isolated bands of transverse muscle fibers are present thruout the body just within the basement membrane. Longitudinal muscles are not so large in the trunk as are the transverse series, but constitute the important muscle system of the tail. The transverse muscles of the tail frequently give a moniliform appearance to that organ, such as is described by Leidy (1877) for *Glenocercaria lucania.*

The nervous system of *C. pellucida* (Fig. 23) varies from the distome nervous system only in its relation to pigmentation and the eye-spots. There are six anterior trunks and six posterior trunks arising from a paired brain center. They constitute the dorsal, lateral and ventral nerve lines. These trunks are carefully followed by the melanoidin pigment fraction. The eye-spots receive

innervation from the dorsal trunks; the paired eyes are innervated from the posterior trunks and the median eye from the fused branch of the anterior dorsales. The optic nerve runs forward from its origin in the dorsalis and enters the pigment cup from above, ending in a sensory cell (Fig. 24). The general anatomy and histology of this eye-spot is similar to that described for all Turbellaria and Monogenea. However, no previous account has been found for the structure of the eye-spot of the Digenea showing its relation to the central nervous system.

Locomotion is brought about thru a coöperation of the body musculature together with the special functioning of the oral sucker and the posterior locomotor pockets. The tail serves as a swimming organ, with a peculiarly rapid and nervous lashing.

Encystment occurs as a final step in the larval stage of the life-history of the hermaphroditic generation, in preparation for entering the definitive host. The process is rapid and the mucoid cyst is secreted by the cystogenous glands before the tail has been thrown off. This organ is freed from the cyst by the violent wriggling which it produces. The cyst is spherical; it encloses the now quiescent larva. The outer portion of the cyst is an opaque mucoid, which gives the cyst an appearance of a white grain, about the size of a pin-head. The larva now waits transfer to the definitive host.

Cercaria konadensis Faust 1917

Cercaria konadensis is a species of monostome cercaria of the binoculate type. The species is more graceful than *C. pellucida*. Its bodily contour is most usually spatulate, while the long tail reaches far behind. The small amount of pigmentation around the two eye-spots and the less usual pigmentation along the nerve trunks caudad serve to indicate the superficial differences between the binoculate group to which this form belongs and the trioculate group.

Cercaria konadensis was found in *Lymnaea proxima* Lea, collected from the Bitter Root River at Corvallis Montana in October 1916. It occurred as an infection along with the larger species, *C. pellucida*. Of the snails examined, 31.3 per cent were infected with this cercaria in the connective tissue between the liver ceca. The cercaria measures 0.4 mm. to 0.46 mm. in length and has a bodily width of 0.1 mm. to 0.16 mm. (Fig. 25). The tail is of equal length under conditions of relaxation, but may be extended so as to exceed by far the bodily length. At its base it has a transverse diameter of 30μ to 40μ. The posterior locomotor organs are not so conspicuously lateral as those of *C. pellucida* (Fig. 4). Considered together with the younger stage of *C. pellucida* (Fig. 12), these pockets suggest an origin from the caudal pockets found in certain distome cercariae. Unlike those of *C. pellucida*, the posterior locomotor pockets of *C. konadensis* are provided with about ten gland cells surrounding the lumen, cells probably of a secretory nature (Fig. 21).

The parthenita (Fig. 26) is a relatively small, elongate redia, 1.7 mm. in length and 0.35 mm. in transverse section near the middle. It is attenuately obtruncate, with the posterior end sloping down to a blunt point. The pharynx is muscular but small, 60μ in cross section, and aspinose internally (Fig. 31). The rhabdocoel gut extends posteriad about three-fifths the body length. The posterior end is filled with cells, composed of a central rachis with apex directed posteriad, and an outer cell complex of goblet cells (Fig. 30). The central rachis comprises the germinal epithelium, the proliferating region of which is situated subterminally. From this epithelial mass the matured parthenogenetic eggs are proliferated forward so that the germ balls come to lie in the lumen posterior to the gut. Similarly to those in *C. pellucida*, only the maturing cercariae come to lie around the gut.

The excretory system of *C. konadensis* consists of the circuitous trunk system, opening posteriorly into a non-muscular vesicular bladder. This vesicle measures 16μ to 17μ in width and 14μ to 15μ along the longitudinal axis of the cercaria. The excretory pore is dorsal, opening from the middle of the bladder (Fig. 29).

The digestive system is of the usual triclad type, with no distinct pharyngeal region.

The genital organs are notocotylid in character, but different in several features from those of *C. pellucida*. The ovary (Fig. 28) is skull-cap shaped, with a distinct Laurer's canal. A short oviduct leads into the ootype. The uterus, emerging from the ootype, runs cephalad, ending in a swollen vagina some distance behind the line joining the paired eye-spots. The vitellaria consist of a double series of five inner and three outer follicular masses. The individual glands are very diffuse and dendritic.

The testes are small, lateral, and posterior to the ovary, with the vasa efferentia describing a broad crescent anteriad around the ovary and meeting in a common tube, the vas deferens, which runs forward to the left and parallel to the uterus. The vas deferens ends in a swollen cirrus pouch (Fig. 25).

The nervous system corresponds to the monostome type described for *C. pellucida*, except that the dorsal trunk to the median pigment eye-spot is lacking.

In the tail six paired groups of gland cells, derived from parenchyma, occupy places just lateral to the median canal of the excretory system, each group dove-tailing into the one next proximal. These caudal glands indicate a much closer kinship of this worm to *Cercaria urbanensis* than to *C. pellucida*.

Encystment is brought about by the pouring out of the contents of the cystogenous cells and by subsequent decaudation.

HOLOSTOMATA

Cercaria flabelliformis Faust 1917

Cercaria flabelliformis is the first larval holostomid to be described in detail for North America. Leidy has listed *Tetracotyle typica* Diesing from

Lymnaea catascopium and *Physa heterostropha* (1890). Rettger (1897) has mentioned a larval tetracotyle in connection with a life-history study, but he has failed to identify the species.

Cercaria flabelliformis was found in three collections of *Physa gyrina* Say, taken from the Bitter Root River in the vicinity of Corvallis, Montana, in October 1916. Practically every snail from these collections bore evidence of infection with the parthenita of this species, altho only 14.7 per cent of the snails examined contained the tetracotyle. The mature cercaria has a length of 0.48 mm. to 0.56 mm., and a width of 0.44 mm. It is about 0.2 mm. thick. While the anterior end is not clearly set off from the posterior end as is usual in holostomids, it does have the suctorial cup which includes all the ventral suctorial apparatus, including among the rest the lateral suctorial grooves. In the young larva these lateral organs are discoidal (Fig. 41); in the mature tetracotyle they have become modified into lateral lappets (Fig. 40).

The larva was found maturing within the redia, free in the liver interstices, and encysted in the liver tissues. It was seldom found free in the tissues.

The parthenita (Fig. 42) is a redia which measures 0.5 mm. in length by 0.052 mm. in transverse section. The head is set off from the trunk by a collar prominence, while in the posterior third of the body are found the "walking feet," which protrude ventrolaterad to support the redia. The posterior end of the body is produced into a large knob, in which are parenchyma and germinal epithelium cells. At the oral end is a wide muscular organ. It is not clear whether it is a pharynx or an oral sucker. It is about 40μ in transsection and surrounds the fore-end of a gut 0.18 mm. long. On the ventral side are two groups of salivary glands, six cells to each group, opening into the anterior region of the gut thru a common duct for each group (Fig. 43). Around the anterior end of the gut, just behind the muscular organ, is a nerve complex (Fig. 42), differentiated into two ganglion masses on the dorsal side, four nerve trunks, and a circumintestinal commissure. A birth-pore is here ventral and slightly sinistral. The wall of the parthenita is heavily covered with an integument of non-cellular material, beneath which are muscle and parenchyma elements. Running thru the parenchyma is a complex diamond-pattern excretory system.

The germinal epithelium is localized at the posterior end of the redia. It offers an unusually fine opportunity for study of the maturation of the ova. The detailed description of this maturation is found in the section on morphology (p. 16).

The germ balls may differentiate into a second generation of rediae and cercariae at the same time. These larvae are about equal in size as they develop, but the cercariae differentiate much more rapidly than do the rediae so that the two are readily distinguished. Usually only three or four cercariae are found developing at one time in the redia, along with many daughter redia. This fact seems to indicate that the animals have come to depend largely on parthenogenetic propagation. The cercariae escape thru the birth-pore and

soon encyst in the free tissue of the host. The second generation redia is already producing germ balls before it comes to take up a free existence outside the first generation redia.

The internal systems of organs of *Cercaria flabelliformis* are of considerable interest. However, since they are described in detail in the respective sections in the morphological division of this paper (pp. 37, 45, 54) they will not be treated here.

Valuable data on holostomid anatomy are obtained by a comparison of *Cercaria flabelliformis* with the following species:

Tetracotyle pipientis nov. spec.

This species of larval trematode was found in March 1917 in the mesentery and pericardium of a large number of *Rana pipiens* collected in the vicinity of Chicago, Illinois. All of the frogs were more or less infected with this holostome. The infection consisted of creamy oval yellow cysts, either single or in grape-like clumps. Each cyst consisted of many lamellae, and innermost, a tough cyst membrane. The inner membrane stains a deep brown with iodine in 70 per cent ethyl alcohol. The gross measurement of the cyst ranges from 0.5 mm. to 0.76 mm. in lesser diameter and 0.7 mm. to 1.0 mm. in greater diameter, while the inner membrane is about 0.3 mm. by 0.5 mm. Within the inner membrane is the larva, tightly coiled at one end of the cavity, while the remainder of the cyst, often two-thirds of the volume, is filled with accumulations of large excretory granules. Some of these granules have fused to form single clumps as large as the larva

When the lamellae and cyst membrane are teased open and the larva is allowed to work its way out, the body becomes expanded and flattened. It then measures 0.5 mm. in length by 0.37 mm. in trans-section (Fig. 47). The oral sucker is 75μ in diameter. It lies in an anterior cone of the body. Anterolateral prominences and the blunt posterior portion of the body give a lyrate outline to the worm. The primitive genital pore, 80μ in diameter, lies in a plane where the anterior and posterior portions of the body join, just within the suctorial pocket. The free ventral wall of this pocket is often folded backward so that it fits down snugly against the body. At other times it bulges out so that the pocket cavity is a large ovoid atrium. The acetabulum is represented by a single lappet situated behind the primitive genital pore. The non-muscular accessory suctorial grooves consist of long narrow slits, directed obliquely inward toward the acetabulum. The entire worm is covered with minute anterior and posterior spines, equally prominent. The primitive genital pore is crowned with a ring of fused spines. The lateral suctorial organs are surrounded by a band of discrete spines imbedded in the tissues.

The worms examined were all filled with excretory granules. A careful study of the larva showed the main course of the excretory trunks to appear as shown in figure 48. The median posterior excretory pore, slightly dorsal, communicates with the bladder which merges imperceptibly with the paired

lateral trunks. These tubes lie just within the margins of the larva and unite with one another in a large transverse vessel at the anterior end of the body, so that a complete circuit is formed. If a rent is produced in the body near the oral sucker, it is customary for the excretory granules to be poured out there rather than thru the natural channel. A tube from the lateral trunks crosses thru the ventral pocket wall at its anterior end. Tributary tubules, bisymmetrically arranged, empty into the main trunks, mostly at the anterior and posterior margins of the body.

The digestive tract is simple and inconspicuous. A small swelling within the oral sucker marks the pharynx, just behind which is the esophagus. The ceca barely clasp the anterior margin of the primitive genital pore.

The genital organs are readily recognized as holostome in type (Fig. 47). They open posteriad. A small spherical ovary lies median. Dorsal to this is the ootype, into which come the short oviduct and the transverse vitelline ducts. The vitellaria are diffuse bands of large follicles extending from the anterior face of the acetabulum to the posterior margin of the genital pouch. They lie strictly ventral. Two large oval testes lie to the sides of the ovary, the one (t_1) slightly anterior to the other (t_2). They have individual ducts (efferent) which reach the genital pouch and fuse into a common vas deferens just before entering the genital pouch. This organ is muscular, oval in contour, with the transverse diameter longer than the longitudinal.

A survey of the literature shows that only one tetracotyle has been reported for Amphibia, *Tetracotyle crystallina* (Rud.), from the mesentery cysts in *Rana temporaria*, *R. esculanta*, *Bufo igneus*, *B. viridis*, and *Vipera berus* (Rudolphi, 1819:380-382). The formation of the cysts is not clearly described, but the large size of the Europen tetracotyle, together with its oval contour, aspinose body and oval accessory sucking discs, clearly separates it from *Tetracotyle pipientis*. The new species conforms much more to the type represented by *T. colubri* v. Linstow, but differs from it in the relative sizes of the oral and ventral suckers, and the possession of small spines all over the body instead of a few broad spines (Linstow, 1877:192; Fig. 22).

While the excretory system is one of the best systems of organs to use in systematic work with trematode larvae, in the absence of such data for other tetracotyles described, the comparative data actually afforded are sufficient in this case to justify the establishment of *Tetracotyle pipientis* as a distinct species.

Observations on the anatomy of *Tetracotyle pipientis* present an opportunity for comparison with *Cercaria flabelliformis*, the parasite of the Bitter Root mollusk, *Physa gyrina*.

The two larvae are about equal in length, but *C. flabelliformis* is considerably the wider. The widest region in *T. pipientis* is in the anterior region of the body; the widest portion of *C. flabelliformis* is in the middle of the body. The suctorial pocket in the former species has grown over the ventral surface so that a true pocket is formed with the opening anterior; in the latter

species the suctorial pocket is hemispherical with the opening ventral. The lateral accessory suctorial grooves in *T. pipientis* are non-muscular oblique slits; in *C. flabelliformis* they are at first oval depressions which are modified later into a pair of lateral lappets. The primitive genital pore in *C. flabelliformis* is 0.05 mm. in diameter; in *T. pipientis* it is 0.08 mm. wide, with a crown of heavy spines. The homologies between the lateral excretory trunks of the two species are apparent, altho the median transverse trunk is much farther anterior in *T. pipientis* than in *C. flabelliformis*. The tributary tubules are entirely different in the two species. The digestive ceca of the Bitter Root species conform to the family type in extending well into the posterior part of the body; those of *T. pipientis* are short and rudimentary. The genital organs of the two species occupy the same relative position, altho individual variations in size and shape of organs are evident.

In concluding the study of the tetracotyle larvae, emphasis must be placed on the maturation of the parthenogenetic ova, which shows that these larvae do not develop in miracidia, without the intercalation of parthenitae as Brandes (1891:572) and Fantham (1916:224) believe. This fact, previously recorded by the writer (1917), makes the morphological evidence complete in support of the view of true alternations of hermaphroditic and parthenogenetic generations among Holostomata.

Cercaria ptychocheilus Faust 1917

This form, really a Diplostomulum, is elongate ovate in outline, with dorsoventral flattening, slight ventral concavity, and a more or less distinct separation of body into anterior and posterior portions. In addition, the group to which this worm belongs lacks the lateral auxiliary sucking grooves which are characteristic of the tetracotyle forms. Several species of Diplostomulum have been well described and their excretory system beautifully traced by von Nordmann (1832). These include the species *D. volvens*, *D. cuticula*, *D. clavatum*, and D. *brevicaudatum*. Of the forms found in North America there have been recorded *D. cuticula*, *D. volvens*, and *D. grande* of the Old World species, and *D. parvulum* (Stafford), new to North America. However, as has been previously suggested, none of these American records give sufficient data to distinguish accurately the species.

The general outline of the body of *Cercaria ptychocheilus* is such as to distinguish it readily from the described species. Broadly oblong-ovoid in contour, with the anterior half laminate and the posterior portion fleshy, this cercaria might at first be confused with distome cercariae. Such a confusion is caused, further, by the abbreviated appendiculate portion of the larva, which, on extension into a caudal cone, may reach one-third of the body length, but on contraction barely protrudes behind the anterior part of the body. The concavity of the anterior part is found only in the fleshy region behind the acetabulum. Here in this area is found the muscular complex comparable to the cup-shaped suctorial apparatus of the tetracotyle.

The Diplostomulum (Fig. 49) measures 0.48 mm. to 0.63 mm. in length by 0.17 mm. to 0.37 mm. in width, and about 30μ thick in the fleshly portion of the body. The oral sucker is small but powerful, and is directed strictly anteriad. Behind this oral region the esophagus is enlarged into the pharynx, about 40μ in section. Behind the pharynx is an equal portion of the esophagus which is non-muscular, posterior to which the ceca rise, spreading out into a broad furculum.

The acetabulum is large and circular; it is situated somewhat posterior to the middle of the body. At times of extreme contraction the acetabulum becomes narrowed antero-posteriorly, with a transverse wrinkling. This disc measures 70μ in diameter. The primitive genital pore, situated just in front of the acetabulum, has lost its connection with the genital system and has become modified into a muscular sucking disc.

The excretory, genital, and nervous systems have been treated on pages 37, 45, 54, as types for the hemistome larva. A comparison of these data with v. Nordmann's observations on *Diplostomulum cuticula*, *D. volvens*, and *D. clavatum*, and with the work of Blanchard (1847) on *Hemistomum alatum* (Goeze) shows the fundamental conformities and differences of the excretory systems of the group. However, the nervous system (Fig. 53) is worked out thoroly in this paper for the first time in the Hemistomidae. The genitalia bear a fundamental resemblance to those of the adult species, as described by Brandes (1891), but differ in size, shape and position of the respective organs. This difference may be accounted for in part by the immaturity of some of the organs, but there are undoubtedly specific differences, such as the lamellae of muscular nature in the genital pouch and the glandular cells emptying into the pouch.

The larva *Cercaria ptychocheilus* was taken from mesentery cysts of *Ptychocheilus oregonensis* Richardson, caught in the Bitter Root River in April 1915 in the vicinity of Stevensville, and Carlton, Montana. Thousands of cysts were found. The cysts are much larger than the larvae (Figs. 50, 51) and are filled with a limpid milky fluid which bathes the larva and serves as a liquid cushion. The cyst is oblong, and flattened. It is composed of a thin, tough membrane, and it is attached to the mesentery by a discoid annulus in the middle of one of the flattened sides. Within the cyst the worm works around and grows, so that it comes to fill the cyst in later life. At frequent intervals there is extruded from the excretory bladder a considerable quantity of granules which pile up at the posterior end of the larva within the cyst, but are soon dissolved and absorbed by the fluid medium.

The encysted animal when placed in a normal saline solution soon increases its activity and bursts thru the cyst. This rent usually occurs at one end of the membrane. The larva then crawls out with a "measuring worm movement." After several hours of activity it settles down on the bottom of the container and remains quiescent, altho slight mechanical disturbances activate

it again. In a modified Ringer's solution ninety per cent of these larvae were kept alive for forty-eight hours.

It seems probable that *Cercaria ptychocheilus* is in an intercalated host.

DISTOMATA

Xiphidiocercariae (Stylet Larvae)

The xiphidiocercariae are grouped together because of their possession in common of a larval stylet. The writer believes that the features of the genital and excretory systems of the group are more fundamental characters which will hold the members of the group together.

Cercaria crenata Faust 1917

Cercaria crenata is a delicate larva, with an ovate bodily outline and a short lanceolate tail (Fig. 55). The body measures 0.25 mm. in length by 0.13 mm. in width, and the tail, 0.15 mm. to 0.16 mm. in length by 20μ to 30μ at the base. The entire body except the tail is covered with minute hair-like spines. A large median spine, the stylet organ (Figs. 56, 57) lies in the dorsal wall of the oral hood. This organ is about 30μ long by 5μ in width at its base. It has the general shape of a quill pen, with reinforcements at its base and also in the distal portion toward the acute point. The distal third of the stylet is bent ventrad about 20 degrees. There are two prominences in the anterior portion of this organ, one where the shaft joins the quill and a less prominent one-half way between this position and the quill point.

The oral sucker is relatively large, 20μ in diameter, while the acetabulum, situated three-fifths the way from the anterior end, measures just half that diameter. The tail is inserted in the posterior caudal pocket which has no spinous projections.

Cercaria crenata was found in large numbers in 13.6 per cent of *Lymnaea proxima* Lea, taken from the springs at Fort Missoula, Montana, in October 1916. It occurs in oval sporocyst sacs, 0.5 mm. in length and 0.35 mm. in diameter. At one end the germinal epithelium, is localized and from this end the ova are proliferated. Only cercariae have been found to develop within the sporocysts.

When the cercaria is mature its breaks thru the wall of the sporocyst and swims thru the surrounding medium. The tail is retained for a considerable time, and encystment is slow. This seems to indicate a considerable period of free-swimming life.

The internal structure of *Cercaria crenata* is such as to distinguish it readily from the other stylet cercariae. The excretory system is characterized posteriorly by a subspherical vesicle, deeply crenate. It measures 20μ long and 30μ wide. Anterior to the bladder a bicornuate trunk empties into the vesicle thru a common median tube. The horns of the U are widely separated. At the place where each main lateral turns forward there is given off a small dendritic tubule, directed posteriad. Some distance ahead of the acetabulum

the main lateral trunk divides into inner and outer tubes, each of which has a number of branches and capillaries. The main tube of the tail is median, with no prominent tubules.

The digestive system consists of an esophagus provided with a pharynx for most of its way, and, behind the pharynx, a typical gut extending to the posterior plane of the acetabulum.

The salivary-mucin glands in *C. crenata* are of a unique type. An outer series of eight small vesicular cells, with a common duct system into the oral pocket, corresponds to the usual salivary-mucin gland system of cercariae. These glands are readily made out in the living worm. An inner series of five cells, two of which are just behind the pharynx and three behind the acetabulum, empty thru a common duct system into the oral pocket. This series is not seen in the living larva, but in stained specimens the cells show small vesicular nuclei with deeply staining cytoplasm and numerous chromophilic granules. This inner series probably consists of a type of salivary gland different histologically and suggests a correspondingly different function.

The genital cell masses are prominent and are well differentiated early in development. Their structure and position are indicated in figure 59. The ovary lies posterior to the acetabulum and median whereas Laurer's canal lies anterior and to the left. The uterus is characterized by a double coil, which ends in a moderate sized vagina, just anterior to the acetabulum. The vitellaria are limited to three cords which lie in a transverse plane just posterior to the ovary. The large flask-shaped testes lie behind the ovary. This genital system suggests the Plagiorchiine arrangement. The distribution of vitellaria is similar to that described by Poirier for *Plagiorchis sauromates* (1886, pl. 2).

Cercaria glandulosa Faust 1917

A stylet cercaria characterized by a multiplicity of glands has received the name of *Cercaria glandulosa*. It is somewhat larger than *C. crenata*, is more oblong-ovate, and is a much more active larva (Fig. 60). The body measures 0.45 mm. in length and 0.2 mm. in width. The tail is slightly shorter than the body, 0.35 mm. in length, by 50μ to 60μ in section at the base. The tail is set within the caudal pocket. This pocket is provided with a pair of locomotor grooves, in which are set a number of stiff spines. Below the insertion of the tail is a small lappet (Fig. 63), provided with three spines directed posteriad. A mucoid secretion is present in the sinuses of the pocket, lateral to the base of the tail.

The stylet organ measures 39μ in length by 5μ in width at the base of the shank. It is reinforced all thru, but especially at the base of the shank, and thruout the quill. The point of the stylet is blunt. The stylet, as well as the entire body, is very delicate, and is shattered by the slightest pressure of the cover slip. The oral sucker is directed downward; it measures 86μ in diameter, while the acetabulum, in the middle of the ventral side, is smaller, with a diameter of 66μ.

The cercaria was found in the liver tissues of *Physa gyrina* Say from the Bitter Root River in the vicinity of Hamilton, Montana, in October 1916. Forty per cent of the physas examined were infected with the parasite. The cercaria develops within a very simple sporocyst, which has a length of 0.34 mm. and a width of 0.17 mm. (Fig. 67). The wall of the sporocyst is delicate, consisting of a single layer of very thin epidermal cells, with no basement membrane and no muscular complement. The genital epithelium is localized at one end, and from this only a few cercariae are developed at any one time.

The excretory system of *Cercaria glandulosa* presents some interesting features. The bladder is flattened, truncate, and subterminal instead of terminal. A narrow canal communicates with the excretory pore which is median posterior. The four angles of the bladder are muscular. When the bladder is emptied these corners lie close together, so that the cavity of the bladder is small. Then by the expansion of the bladder this organ is filled from the trunks (Figs. 64, 65). Two vesicular cornua empty into the bladder. Each cornu is directed laterad and slightly anteriad; it soon constricts to form the lateral tube. The common tube divides soon to form the posterior tubule and the anterior tube. The anterior vessel then divides in the region of the acetabulum to form a trifurcate system. Just behind the region of this division there is a small vesicular swelling where granules of the system accumulate. The excretory system in the tail consists of the common median vessel and several tributaries.

The digestive system is characterized by an abundance of glands, so that the entire tract is surrounded with gland cells. A small pharynx surrounds the esophagus near the anterior end of the tube. The esophagus extends to the preacetabular region, at which place it forks to form short furcae which barely clasp the anterior end of the acetabulum. Along this entire course there are many gland cells in clusters, especially abundant in the pharynx region. Their relation to the pharynx and nerve ganglia is shown in figure 72. The individual gland cell is ovate, with a short neck. The cytoplasm is chromophilous. There is no recognizable duct connection thru the myoblasts of the pharynx to the lumen. The nuclei of these cells are large and studded with granules.

In addition to the grape-like clusters of gland cells surrounding the entire digestive tract there are right and left paired gland groups of the salivary-mucin type. They consist of nine large cells to each group, usually situated in the acetabular region, but capable of extension, so that they may lie as far caudad as the bladder (Fig. 62). Figures 73 and 74 show sections passing thru the anterior tip of the excretory vesicle. In each of these a right and a left gland are visible. In these glands not only is the nucleus granular, but the cytoplasm is densely granular, the granules being assembled in little clumps. Frequently (Fig. 73) there are vacuoles within the cytoplasm.

The genital organs are represented by cell masses which show clearly the location of the mature organs, but as yet show little differentiation (Fig.

66). Ovary, Laurer's canal, vagina, uterus—all are recognized in the midacetabular region, with vitelline follicles extending from the oral aperture to the posterior end. They are divided into anterior and posterior portions. No testes are yet to be found. The genital organs as a whole seem to indicate Plagiorchid relationship.

Conspicuous thruout the body are the large bundles of longitudinal muscle fibers. They are scattered thruout the parenchyma at the anterior end (Fig. 72), while they are much larger and more concentrated laterad in the region of the acetabulum. Still further caudad they become fewer and less conspicuous (Fig. 74).

The nervous system has been described in detail on page 51.

This cercaria lives a free-swimming existence for only a short time. When placed in a watch-glass in tap water, it soon drops its tail, preparatory to encystment. The tail is helpful in locomotion, yet after decaudation this species is more active and able to cover considerably more ground than most other species with the aid of the tail. This movement is due in no small measure to the spines in the locomotor grooves of the caudal pockets. After moving about for a little while the cercaria settles down and pours out an abundance of slime within which it coils up and becomes quiescent until a transfer to the new host is effected.

Cercaria diaphana Faust 1917

Cerceria diaphana is closely related to *C. glandulosa.* When contracted, it is broadly ovate (Fig. 78), but on extension it assumes an elongate ovoid contour (Fig. 76). The measurement of the body when at rest is 0.2 mm. to 0.26 mm. in length by 0.1 mm. to 0.12 mm. in width. Under pressure of a cover slip the internal organs are beautifully worked out and the delicate mist of the parenchyma in which they are imbedded suggests the term "diaphanous." The tail is broadly lanceolate, 0.15 mm. in length by 0.04 mm. at the base. It is inserted into a caudal pocket provided with spinose locomotor pocket grooves. The spines are few in number (8 to 10) and well developed. They are directed meso-caudad. As in *C. glandulosa* the two sinuses of the caudal pocket are thickened by a mucoid lamination. The acetabulum is situated in the middle of the ventral side; it has a diameter of about 32μ. The larger and more powerful oral sucker has a diameter of 44μ. The stylet organ (Fig. 77) is a delicate but firm quill of 39μ length and 5μ width at the base of the shank. It is entirely without any reinforcement in the region of the shank but has thin ventral plates at the junction of the shank and quill, while inserted in the quill point, directed posteriad, is a minute spine, 5μ long and 0.5μ in diameter.

Cercaria diaphana was found in the liver tissues of *Lymnaea proxima* in the Bitter Root River near Corvallis in October 1916. The infection was heavy. The cercaria develops in an oblong sporocyst (Fig. 79), frequently drawn out or contorted at one end (Fig. 80). The unique feature of the

sporocyst is that the germinal epithelium is not localized; consequently germ balls may be derived from any portion of the body. Whether or not the germ cells arise parthenogenetically has yet to be determined. This type of germ ball production represents a structural simplicity previously not recorded for the sporocyst.

The excretory system differs from that of other stylet cercariae mainly in the shape of the bladder and of the essential tubes. The bladder is small, heavily muscular, flattened antero-posteriad. Leading out from it in a median plane is a non-muscular shank of some length, which opens into two cornua a considerable distance in front of the bladder. Caudad these cornua are vesicular, but further cephalad they become constricted into a system of tubules similar to those of *C. glandulosa*, which run thru the body to collect the excretory wastes.

The digestive system consists of a long esophagus, with pharynx at the anterior end, and a wide bifurcation somewhat anterior to the acetabulum. The entire digestive tract is very attenuate in outline. It is not supplied with glands along the furcae but has an even more abundant supply than *C. glandulosa* in the region of the pharynx (Fig. 76). Altho the pharynx itself measures only 15μ in cross section, the glandular area as a whole embraces a sphere 65μ in diameter. The rest of the tract is free from gland cells of this nature. The salivary-mucin glands are situated in the upper outer reaches of the furcae. Each group consists of eight cells, relatively very small, granular, with a common duct system opening into the oral pocket.

The genital organs are similar to those of *C. glandulosa* (Fig. 78). They differ from the genital cell masses of that form in the more limited vitellaria, and the more conspicuous Laurer's canal. This form is probably a Plagiorchid larva.

Unlike *C. glandulosa* this cercaria is slow to drop its tail and much slower to encyst, in spite of the fact that there is an equally good pair of posterior locomotor pockets with spines and an equally good supply of cystogenous material. We have here, then, evidence of a physiological adaptation to different conditions of the environment, where the structure of the two types would lead one to expect similar habits and reactions.

Cercaria dendritica Faust 1917

Cercaria dendritica is a species of cercariae readily recognized by its obovate structure, large suckers, large muscular pharynx, and large muscular excretory vesicle. The body as a whole is heavily muscular. The tail is short and almost conical (Fig. 81). The body measures 0.33 mm. to 0.4 mm. in length by 0.13 mm. to 0.17 mm. in width. The tail is about half the body length, 0.16 mm. and is 0.04 mm. wide at the base. It is inserted into a typical caudal pocket, the whole cavity of which is lined with stiff spines. The large oral and ventral suckers are nearly equal in size. The former has a diameter of 62μ and the latter of 60μ. The stylet (Figs. 82, 83) is short and stout, heavily reinforced at the shank, with a flat deltoid quill. The quill

is pointed at the tip. It is directed ventrad by about ten degrees more than the shank. The stylet has a length of 44μ and a breadth at the base of the shank of 14μ.

Cercaria dendritica was secured from two collections of *Lymnaea proxima* taken from the chara sloughs at Fort Missoula, Montana, in October 1916. The infection was in the liver interstices. The parthenita (Figs. 87-89) is a well-developed sporocyst, with an attachment disc, but without any indication of a digestive tract. It seems to approach a redia more nearly in its structure than any other described sporocyst. The sporocyst is muscular and heavily covered with integument. The parthenogenetic eggs develop from a germinal epithelium situated at the antipodal end from the disc. The stages of cleavage are clearly made out from the study of the germ cells proliferating from the germinal epithelium (Fig. 89). This layer is closely pressed against the epidermis. As the cells mature they increase in size. The increase continues thruout the cleavage, so that a three-cell stage is larger than a one-cell stage, and a morula is larger than a five-cell stage. This continued growth of the embryo is accounted for by the nourishing medium which bathes the sporocyst. This is a special case of nurture, where the growth stimulus is reacted to immediately. The germ ball attains a considerable size before it begins to differentiate, altho epiboly has occurred soon after the morula stage has been reached. The animal is mature before it breaks thru the wall of the sporocyst and swims out into the inter-cecal spaces.

The larva has an interesting excretory system (Fig. 81). An immense spheroid bladder, somewhat crenate, opens dorso-posteriad thru a small pore. Anterior it receives the contents of two large muscular cornua thru a common opening. These cornua extend laterad to the extreme margin of the animal. At the outside of each, at the margin of the worm, arise three tubes, one directed posteriad and two directed anteriad. The capillaries are dendritic. The caudal tube is a median canal without any prominent tubules.

The alimentary system consists of a pharynx with muscular fibers developed early. It has a width of 30μ and a length in section of 36μ. A short, attenuate esophagus opens posteriad into two vestigial furcae. Anterior and lateral to the acetabulum are the salivary-mucin glands, eight to each group. They are moderately large (Fig. 85), and empty thru common duct systems into the oral pocket.

The conspicuous features of the genital system (Fig. 86) are the large swollen vagina, and the prominent Laurer's canal, the latter extending out on the left side of the acetabulum under its posterior margin. In the mid-area, just behind the acetabulum, are two small pyriform testes. The vitelline glands extend from the extreme anterior margin of the worm to the extreme posterior end; they are attenuate, sparsely branching serpentine chords, composed of a long anterior and a short posterior portion. The vitelline ducts run in from the postero-lateral regions to the ootype, which is just anterior to the testes. This type is suggestive of Plagiorchid relationships.

Soon after the cercaria is set free into the water, it drops its tail. Almost before the observer is aware it secretes a thin membrane from the abundance of cystogenous material contained in the large cyst cells which pack the parenchyma of the worm. The oval cyst with the worm coiled up inside is shown in figure 84. This type of cyst offers only a temporary lodgement for the cercaria, and it is evident that the worm must reach the definitive host soon if the infection is to be successful.

Cercaria micropharynx Faust 1917

Cercaria micropharynx is a minute larva of the xiphidiocercariae, oval in contour, with small clavate tail (Fig. 93). The body is covered with minute spines arranged in diamond pattern, progressively less prominent toward the caudal end. The spines are probably constant characters of the adult as well as of the larva, since the entire trunk is well supplied with these spines while the tail is naked. The body measures 0.18 mm. in length and 0.09 mm. in width. The tail is 0.14 mm. long and 0.03 mm. at the base. It is inserted into a caudal pocket provided with a group of spines on the lateral lappets ventral to the tail. The oral sucker is large for the body size, 35μ in diameter, while the acetabulum is slightly smaller, 30μ in diameter. Inserted in the hood of the oral sucker is the stylet organ (Figs. 91, 92), 34μ long and 5μ to 6μ in breadth along the shaft. The organ is reinforced all around and has a velum stretched across the ventral surface of the quill.

The cercaria was secured from the infected liver tissues of a large number of *Lymnaea proxima*, taken from Rattlesnake Creek, Missoula, in November 1916 and in May 1917. The cercariae develop in oval irregular sporocysts, measuring 0.24 mm. along the long axis and 0.18 mm. along the short axis (Fig. 94). The body wall of the sporocyst consists of a single layer of epidermal cells, between which are found numerous excretory granules, lying in irregular grooved channels. There is no localization of the germinal epithelium, so that germ balls arise from all portions of the body wall and, when mature, break out into the body lumen. Not only do the cercariae develop to maturity in the sporocyst, but in some cases they drop their tails and encyst in the sporocyst (Fig. 95). Thus the larval host, the snail, is the food of the intercalated or of the definitive host, since no free-living stage is commonly found. In case the cercaria is pressed out of the sporocyst before encystment, it swims about for a very brief period, then drops the tail and encysts.

The excretory system consists of a subspherical vesicle and bellows-shaped cornua, which open into the vesicle thru a common cylinder. The three usual tubes of the excretory system are present, the single posterior and the two anterior ones. The tail tube is single median, with a few inconspicuous lateral tributaries. The cornua are filled with excretory fluids; they are lined with cells (Fig. 98).

The digestive system consists of the very minute pharynx in the midregion of the esophagus, and two vesicular furcae considerably anterior to the

acetabulum. No glands occur in the pharynx or cecal regions, but in the prepharynx region, just within the oral aperture, is a band of about fifty goblet cells of a glandular nature. The salivary-mucin glands are found at the sides of the acetabulum. They consist of eight cells for each group. They are relatively large, vesicular, and have common ducts opening into the oral pocket. In addition to the usual transverse and longitudinal systems just within the integument (Fig. 97, 98), large muscle elements are scattered thruout the parenchyma.

The genital organs (Fig. 96) consist of a prominent vagina, a well-defined Laurer's canal, and a group of massed organs in the vicinity of the ootype. In addition, there are the yolk follicles, distributed over a wide range of the dorsal side of the animal. The follicles are closely massed together. This species suggests a Plagiorchid genital system.

Cercaria racemosa Faust 1917

Cercaria racemosa belongs to that group of stylet cercariae usually designated as *cercariae ornatae*, by virtue of their possession of a fin-fold structure to the tail. While this separation may be concomitant with a deeper, more fundamental difference of type, it is well to bear in mind that fin-folds occur in other groups, such as in monostomes, *Cercaria lophocerca* (Filippi, 1857:5; Fig. 3), echinostomes, *Cercaria echinatoides* Fil. (La Valette:1855,Taf. I, C), and among the furcocercous larvae, *Cercaria cristata* (La Valette, 1855,Taf. II, K). It may be looked on as a modification of the caudal organ for swimming.

The body of *Cercaria racemosa* is elongate ovoid, measuring 0.29 mm. in length by 0.11 mm. in width (Fig. 100). It is characteristically broadest just ahead of the acetabulum. The tail consists of a central lanceolate region and a lateral ruffled fringe, which is most conspicuous at the distal end. The tail measures 0.22 mm. in length and 0.04 mm. in width at the base. It is inserted into the posterior extremity of the trunk, altho there are no lateral sinuses to be found in this caudal pocket. The acetabulum is slightly caudal to the middle of the body. It measures 26μ in diameter, while the larger oral sucker has a diameter of 36μ. The stylet organ (Figs. 101, 102) is delicately attenuate, with a reinforced tip. It is 27μ long and about 5μ wide at the base.

The species was found in the liver of *Lymnaea proxima* in the chara sloughs of the Bitter Root River at Fort Missoula, Montana, in October 1916. It occurred as a minor infection along with *C. dendritica* and *C. gracillima*. The parthenita is an irregular polygonal sporocyst about 0.62 mm. long and 0.38 mm. thick (Figs. 104, 105). At one end is situated a pocket of glandular cells which attach the sporocyst to the host. This is done by the exudation of a mucus. It is doubtful if these cells are at all muscular. At the antipodal end is the germinal epithelium, from which germ balls arise. Only a few cercariae develop within the sporocyst at any one time.

The bladder of the excretory system is truncate, with a common median vessel leading into it from the anterior end. Lining the vesicle at the anterior

end are six gland cells, paired right and left. They appear as small tubercules suspended from the anterior wall of the vesicle. Anterior to the median vessel are two cornua, elongate, yet swollen, reaching antero-laterad around the acetabulum. Near the acetabulum there are received the common posterior and the two anterior tubules. The pattern of the capillaries is racemose. The tail trunk system consists of a common median vessel with many lateral tubules. The entire system is filled with minute excretory granules.

The digestive system consists of a very long esophagus, near the anterior end of which is the small sphincter, and from the posterior end of which the furcae arise. They extend partly around the acetabulum. The salivary-mucin glands consist of right and left paired groups of cells, eight to the group, with long ducts leading in a common bundle to the oral pocket.

In the region of the cerebral ganglion a pair of oval bodies, the non-pigmented eye-spots are located. They are degenerate, similar to those eyes described for *Cercaria gracillima* (p. 52).

The genital cell masses are found in the region of the acetabulum (Figs. 104, 107). To the left is Laurer's canal, and running dextro-laterad is the closely coiled uterus. The genital pore is on the right of the mid-ventral line, anterior to the acetabulum. Running into the ootype from the postero-lateral angles are the vitelline ducts, connecting the vitellaria with the ootype. The testes are not well defined. The relationship of the cercaria is not evident from the genital cell masses.

Cystogenous cell glands are present, altho not as conspicuous as in *C. glandulosa* or *C. micropharynx*. Encystment takes place after a considerable period of free swimming life. Decaudation always precedes encystment. The cyst wall is thin; the animal is easily viewed thru the cyst.

Echinostome Cercariae

Cercaria trisolenata Faust 1917

Cercaria trisolenata represents a unique type of echinostome larva (Fig. 109). It is more attenuate than the average species of this family, and has an unusually short tail. The body has an average length of 0.45 mm. and a width at the preacetabular region of 0.1 mm. The tail is about 0.2 mm. long, lanceolate, and measures 0.06 mm. at the base. An anterior region of the trunk, measuring 0.06 mm. along the median line, constitutes the head region, behind which is a neck-like constriction. There is a collar of 36 spines along the margin of the head, arranged in a single irregular series (Figs. 110, 111). These spines are bluntly rounded at the base and taper to a rounded point at the distal end. They are from 12μ to 14μ in length. The body as a whole is usually covered with minute spines. The acetabulum is beset with an irregular arrangement of crooked spines (Fig. 112). The oral sucker is small but powerful, 33μ in diameter. The acetabulum, situated behind the mid-plane of the body, measures 42μ.

These cercariae, together with *Cercaria gracillima*, are the most cosmopolitan species of the Bitter Root River. They occur in *Physa gyrina* from the

upper and lower reaches of the Valley, and in *Planorbis trivolvis* from the region of Buckhouse Bridge. The infection of the host is always heavy, both as relates to numbers of individuals infected and the number of parasites in the individual host. The per cent of infection ranges from 22 to 100. The parasite is located primarily in the interstices of the liver, but frequently invades the cecal walls and does great injury to the tissues.

The cercaria develops in a redia of well-marked characters (Fig. 117). The redia measures about 1.0 mm. in length and has a mid-diameter of 0.22 mm. and a gross width of 0.35 mm. across the region of the locomotor feet. A small powerful pharynx at the anterior end opens into the rhabdocoel gut which fills the greater part of the body cavity, extending almost to the posterior extremity. The germinal epithelium is at the posterior end. From this layer the ova develop, which grow into cercariae. The first character of the germ ball to become differentiated superficially is the oral sucker (see series of stages in figure 114). Later the tail and the acetabulum become marked off, and finally the oral hood.

At the posterior end a small, non-muscular, truncate bladder is situated. It opens anteriad into two simple unbranched tubes. These can be traced cephalad inside the intestinal ceca to the head of the worm. The cephalic end of the excretory system is unique. Lateral to the pharynx, a triangular channel-system is found. From the anterior angle a small capillary leads forward to a single flame cell. From each of the other two angles a small capillary leads back to a flame cell. This constitutes the trisolenate system at the anterior terminus of the excretory tract. The tail excretory tube is a single median structure and has no laterals or terminal outlet. This fact necessitates a revision of the scheme proposed by Cort (1915:37), in which this writer characterizes the excretory system of echinostome cercariae as "opening on each side of the anterior part of the tail." It seems from the present investigation that the three flame cells in the anterior part of the trunk may be a more reasonable criterion for distinguishing the excretory system of this group. Further work on other forms must be done before this can be definitely proposed.

Excretory granules fill the lateral excretory trunks from the pharynx region as far caudad as the acetabulum.

The digestive system is simple. It consists of a long esophagus, with a very small pharynx sphincter about in its middle, and two very long furcae, extending to the sub-caudal region.

The genital cell masses are yet very immature. There are four cell masses present, one on the upper right of the acetabulum (Fig. 130), the vagina; one behind the acetabulum (Fig. 131), the ovary, and two tandem masses in front of the bladder (Fig. 120), the testes. In the vicinity of the ovary are numerous vitelline follicles, but they have not been found to follow any definite pattern.

The nervous system of this species has been made the basis of the discussion on page 49, and needs no further consideration here.

The musculature is almost all parietal, except for the walls of the intestinal tract. Parietal and splanchnic muscles are similar in structure. The former consist of external transverse and internal longitudinal bundles, while the latter consist of external longitudinal and internal transverse fibers (Figs. 118, 119). Each fiber can be traced to a myoblast, the central figure of which is the large oval nucleus, with karyosome and radiating processes, so that the whole figure appears stellate. There are several fibers originating from each myoblast; they always run along a single axis. The longitudinal muscles of the tail are prominent (Fig. 133).

The body is filled with a parenchyma complex, consisting of undifferentiated cells, connective tissue fibers, and cystogenous gland cells. In the tail of an immature cercaria (Fig. 133), there is a partition of parenchyma cells, separating the caudal excretory canals into right and left tubules. This condition disappears as the animal matures, altho vestiges of these cells may be found in the mature cercaria.

The cystogenous cells are differentiated parenchyma cells, filled with a mucoid in the form of oval granules. In the ordinary cystogenous cell (Fig. 113), the granules are about 1μ by 0.6μ in section. There is a central nucleus to each of these cells, with poorly defined membrane separating it from the cytoplasm. It is conspicuous because of its large number of chromatic granules, composed of elongate flecks. These flecks are also present in considerable numbers thruout the cytoplasm; they are especially massed against the cell walls. The glands are best developed in the middle of the body (Fig. 109, sections *bb* and *dd*). Since the cystogenous glands are well developed, the cyst wall is heavy (Fig. 115, A-C). In crawling over the surface of any object the mature cercaria squeezes off the tail by a constriction of the posterior transverse muscles. A final jerk of the tail frees it from the body. Immediately the cystogenous glands pour out a mucus around the contracting worm, so that at first an oval cyst is formed. Later, as it hardens, it assumes a more spherical outline (Fig. 116). Thru this cyst membrane the excretory and digestive systems of the body and the collar spines are readily distinguished. The cysts are so well walled and so numerous that they suggest a considerable period of wintering over.

Cercaria biflexa Faust 1917

Cercaria biflexa belongs to a type of echinostome cercariae distinguished by a smooth body outline, a long powerful tail, blunt oral hood spines and a reflexed excretory tube. The excretory system worked out by Looss (1894: Fig. 191*c*) for *Distomum echinatum* approaches the system in this species to some extent, but differs from it in many details.

The body of *Cercaria biflexa* is elongate ovoid, with a slight constriction just behind the oral hood (Figs. 134, 135). Both the body and the tail are extraordinarily muscular. The body measures 0.45 mm. to 0.5 mm. in length

and 0.13 mm. to 0.15 mm. in width. The tail is at least as long as the body or slightly longer. Its width is about 0.05 mm. at the base. The oral sucker has a diameter of 55μ and the ventral sucker, situated at the beginning of the posterior third of the body, measures 65μ in diameter. Around the oral hood is a circlet of collar spines, 42 in number, ovoid elongate, bluntly rounded at both ends, with a length of 10μ to 15μ and a thickness of 3μ.

The worm was found in *Physa gyrina* in November 1916, and in *Planorbis trivolvis* in May 1917, in the neighborhood of Buckhouse Bridge, near Fort Missoula, Montana.

The parthenita is a redia with a length measurement of 0.4 mm. and a thickness of 0.088 mm. (Fig. 137). The locomotor feet are short, blunt processes in the posterior third of the body, and have a gross span of 0.1 mm. In contrast to the large gut-pouch of *Cercaria trisolenata* parthenitae, the rediae of this species have short inconspicuous rhabdocoel guts, only 0.1 mm. in length. One-third of this is occupied by the pharynx. The body wall is covered with a thick integument, within which is a heavy muscular layer. At the posterior end are a number of small spinous projections (Fig. 141). The germinal epithelium also is at the posterior end. A noticeable feature of the cleaving ova is their flattened condition (Fig. 141). Stages in maturation and cleavage are seen in this figure and may be compared with similar stages of maturation and development in *C. trisolenata* (Fig. 140.) The cercariae, when mature, escape thru the birth-pore situated ventrolaterad.

A prominent excretory system is found in this cercaria (Fig. 135). The vesicle is a cylindrical organ inflated posteriorly. It is not muscular to any marked degree. Tubular cornua empty into the anterior end of the bladder. As these cornua are traced forward lateral tributaries are found to empty into them at regular intervals. In the region of the pharynx the tubes become attenuated and bend twice upon themselves (Fig. 138). The detailed description of this anterior end of the system of *Cercaria biflexa* is found in the section on morphology (p. 40). It may be noted here that there are three flame cells along the course of the ultimate tubule of the system, and that these seem comparable to the three flame cells found in *C. trisolenata*. The excretory tube in the tail is a single median tube for about two-fifths of the way distad, at which point it forks and continues double the remainder of the way distad, with numerous cross-anastomoses. It does not open to the outside either on the sides or end.

The digestive system consists of an extremely long esophagus, extending all the way to the acetabulum; furcae which end at the caudal end of the animal; and salivary-mucin glands, developed to a very high degree. These latter consist of an inner and an outer series of right and left groups (Fig. 134). There are from fifty to sixty cells in each group, in oblong clusters, with a common duct anterior to each series leading cephalad. The two ducts of each side fuse to form a single lateral duct which leads into the oral pocket. These glands are different from the majority of mucin glands in being differentiated

into inner and outer series. The condition is similar in part to that in *Cercaria crenata* (Fig. 55), in which species there is also a double series of glands on each side of the esophagus. But in this case the glands of the inner and outer series are not different in structure and function as in *C. crenata*. Here, too, the ducts are not composed of a bundle of separate ducts, as is found in *C. marcianae* (La Rue, 1917:5), but consist of a single common duct for the entire group of gland cells.

The genital system is much further developed in this species than in *C. trisolenata* (Fig. 139). Behind the acetabulum is the ovary, from which a uterus leads around the acetabulum, ending in a swollen vagina in the pre-acetabular region. Only the transverse ducts of the vitelline system are differentiated. Behind these are the two testes, unequal in size, one above the other.

The encystment of *Cercaria biflexa* is similar to that of *C. trisolenata* in that it depends on the secretion of mucoids from a large number of cystogenous glands in the parenchyma. It differs, however, in the two species both as to time and place of encystment. *Cercaria trisolenata* encysts only after it has escaped from the liver tissues of the host. *C. biflexa* encysts within the host, immediately upon breaking thru the birth-pore of the redia. Thus a section of *Planorbis trivolvis* liver tissue shows the interstices of the liver ceca filled with encysted cercariae, which continue to grow and differentiate within the primary host (Fig. 159).

Furcocercariae

Cercaria gracillima Faust 1917

Cercaria gracillima is a furcocercous cercaria more slender than those previously described. This species, together with *C. tuberistoma* (p. 82), constitute the second instance of furcocercous cercariae to be described for North America, the first being *C. douthitti* Cort (1915:50-52; Figs. 55-64). In addition to the forked-tail character of these three species, they lack a pharynx, and have paired salivary-mucin glands leading into the oral pocket, composed of four or more cells to each group. The "eyelet" excretory anastomosis, connecting the excretory system of the body and the tail is also a common character.

Cercaria gracillima has an oblong cylindrical body (Fig. 142). The branched portion of the tail is elongate lanceolate. The body length varies from 0.13 mm. to 0.16 mm. and the diameter of the worm varies from 0.02 mm. to 0.03 mm. The unbranched portion of the tail is about 0.16 mm. long and the caudal rami are of equal length. The former is 0.02 mm. to 0.03 mm. in diameter and the ramus has a width of 0.01 mm. The trunk is characterized further by the absence of a true oral disc, while in its place there is an invertible sucker. A ventral sucker, 12μ in diameter, varies in location, according to the movements of the animal, from the middle of the ventral side to a position considerably farther forward. The cephalic region is ovately rounded when the sucker is fully distended and is crowned by a cap of small spines. A

feature of this cercaria, in common with that of *C. douthitti*, is the possession of eye-spots (Figs. 144, 150). But the eye-spots of *C. gracillima* are the more vestigial, for they have no pigment.

This species was found in the livers of *Physa gyrina* Say, collected from the lower reaches of the Bitter Root River near Maclay Bridge, Buckhouse Bridge, and the sloughs at the Roadhouse, near Fort Missoula, in the fall of 1916. In addition it was found in the livers of *Lymnaea proxima* Lea from Rattlesnake Creek, Missoula. The infection in most cases was not exceedingly heavy, except in the collection from the sloughs at the Roadhouse, where thirty-three out of seventy-one individuals were infected, or 46.5 per cent.

The cercariae develop in long cylindrical sporocysts, varying in length from 0.25 mm. to 0.1 mm., but most frequently averaging about 0.5 mm. (Figs. 146, 147). In diameter the sporocysts vary from 0.2 mm. to 0.4 mm. The parthenita is a simple structure, non-muscular, depending on the daughter cercariae for its movement. At one end (Fig. 147) is a non-muscular attachment area; at the other end, merely a rounded non-differentiated cap. The germinal epithelium is localized at the attachment end. From this mass the daughter worms develop. Internal pressure from the developing larvae increases the length and diameter of the parthenita. In development (Fig. 148), the ovoid germ ball first differentiates a tail portion; later the rami appear. It is not until considerably later that the acetabulum is found. The oral spines appear only when the larva is mature.

The movement of the cercaria is characteristic for furcocercariae. The main movement consists in a very strenuous beating and lashing of the rami, so that the head is pushed into the object with which it comes in contact. In case the head is not forced into the object, the worm is set free by a backward movement of the tail and the entire worm squirms around until it comes in contact with another object, when the same boring movement is again attempted. The oral end of the cercaria is much better adapted to this type of invasion of the tissues to be infected than if it possessed an oral disc.

The excretory system of *C. gracillima* is embryologically a single paired system for both body and tail. As development and differentiation of parts progress the tubes in the posterior extremity of the trunk and the anterior region of the tail fuse, to form a median bladder and the common tube of the proximal region of the tail. There remains the bifurcated portion in the laterals of the trunk and the rami of the tail, and in addition, the "eyelet anastomosis." This eyelet structure has been observed by Looss (1896:172-174; Pl. 15), in *Cercaria vivax* Sons, and by Cort (1915, Fig. 57) in *C. douthitti*.

The excretory system in the body consists of two lateral tubes that diverge from the bladder and can be traced forward, together with dendritic tubules and capillaries, the internal ones of which frequently form chiasmic anastomoses across the median plane of the body. Slightly posterior to the middle of the body the lateral tube expands and opens into a pocket provided with

cilia (Fig. 145). These cilia come from a flame cell bordering on the lumen of the lateral tube. A second pocket somewhat anterior is an atrium into which many of the capillaries empty; it is filled with small excretory granules, in this way acting as a secondary reservoir.

The digestive system of *C. gracillima* consists of an unbranched esophagus without a pharynx sphincter, a pair of short degenerate furcae extending posteriad beyond the acetabulum, and a ring of gland cells in the region of the esophagus where the pharynx might be expected. Opening into the oral atrium thru common bundles of ducts are the salivary-mucin glands (Fig. 144). These glands are very large with vesicular nuclei. They are situated in the posterior third of the body. In cross section the ducts are similar to those described by Cort (1915, Figs. 59-62) for *C. douthitti.*

The nervous system has been discussed on page 54.

The genital cell masses in the cercaria are hermaphroditic (Fig. 149). Anterior to the acetabulum are the vagina and the cirrus pouch buds, and lateral, extending both anteriad and posteriad, are the vitelline follicles. In the posterior extremity is a conical germinal mass, from which are proliferated anteriad a number of small testicular follicles.

The general features of this fluke make it possible to refer it to the Schistosomatidae.

Cercaria tuberistoma Faust 1917

This species of cercaria is shorter and much more muscular than *C. gracillima.* The body is elongate ovoid, with the anterior end slightly constricted and crowned with a pair of tuberosities (Fig. 155). The body length is about 0.2 mm. and the width 0.05 mm. to 0.06 mm. The tail measures about 0.32 mm. as a whole, equally divided into common portion and rami. There is no oral suctorial disc, but instead the oral invertible proboscis. The acetabulum measures 0.03 mm. in diameter.

The cercaria was secured from a single light infection of *Physa gyrina* collected in the Bitter Root River at Corvallis, Montana, in October 1916. Out of nineteen snails examined only one was infected. Only a few cercariae were secured, and these were studied as live mounts. From this study the excretory, digestive and general body features were worked out.

The cercaria develops in an elongate, dumb-bell-shaped sporocyst, spreading out at one end to form an attachment disc (Figs. 157, 158). At the end opposite the attachment organ the cercariae develop from the maturation of the germinal epithelium. They escape thru a rent in the wall of the sporocyst. Stages in development (Fig. 158, A-E) are similar to those described for *C. gracillima* (Fig. 143). On the whole the embryos of this species are stouter than those of *C. gracillima.*

The excretory system has the features common to all furcocercariae. The bladder and the eyelet are muscular (Fig. 155). The lateral tubes are of small diameter, with anterior and posterior tubules. No anastomoses take

place in the cercariae of this species. The median tail tube receives six lateral tributaries, the anteriormost of which is reflexed. The rami have each an unbranched tubule.

The cephalic region is marked by a large invertible sucker, extending thru the anterior third of the body. No intestinal ceca whatever have been observed in this species. No glands surround the esophagus as a distinct ring, altho the entire esophageal tube lining is glandular in nature. Four small salivary-mucin glands are situated in the posterior third of the body (Fig. 155). Their thick ducts empty into the oral cavity as heavy bundles. The cells of this system are filled with closely aggregated, deeply staining granules. The nucleus of the salivary-mucin gland cell is extremely small.

This species possesses neither pigment eye nor eye-spot without pigment.

Encystment has not been observed in this species.

Cercaria tuberistoma is probably a schistosomatid larva.

PATHOLOGY

The infection in any case of internal parasitism suggests an inquiry as to the effects of the parasite on the host. The injury on the human subject produced by trematode infections has been the subject of numerous observations and records. Notable among these are the contributions of Looss (1913) on *Schistosoma haematobium*, Katsurada (1914) on *Schistosoma japonicum*, and Ward (1909) on *Fasciolopsis* spp. Again, the effect of trematodes on their host has been the subject of considerable study in fish infection, on account of the economic importance of the problem. But where the special incentives to the problem have been lacking, very little study has been made on the pathological significance of trematode infection.

The helminth parasite causes a two-fold injury to the host, mechanical and chemical. The inclusion of parasites within the organs of the host is the occasion for distension of the organs and consequent irritation; the piercing of organs of the host by the armature of the worm, an actual mechanical injury. These injuries are accompanied by the formation of fibromata within the organs and, usually, attempts to isolate the parasite by the secretion of a cyst around it, as in schistosomiasis (Bovaird and Cecil, 1914:191). In the ordinary infection a toxin is secreted by the parasite, and frequently an antithrombin and a hemolysin are produced. Such injuries as these in higher animals are diagnosed by the blood-picture, where excessive hemocytolysis and eosinophilia are found.

The infected organs of the molluscan hosts of the Bitter Root Valley are the liver ceca. Altho these lie next to the testes, the worms have never been found to invade these organs. Thomas (1883:114) found that the cercariae of *Fasciola hepatica* live normally in the pulmonary chamber of the snail *Lymnaea trunculata*. Cort (1915) found the infected organs of the Campelomas were the gills, but in other species, the liver tissues were the seat of the infection. The infected tissue of the Venezuelan snail, *Planorbis guadelupensis*, is the testicle according to observations made by the writer.

The liver ceca consist of polygonal lymphocytoidal cells grouped around the lumina of the ceca, with an epithelial lining surrounding the ceca. Among the ceca are large interstices filled with lymph. These intercecal spaces are the places where the worms are first found, suggesting invasion thru the blood stream. In light infections, the parthenitae lie here, absorbing the nourishment from the surrounding liquid in which the worm is bathed. The only mechanical injury up to the time of the activity of the cercariae is caused by the agitation of the developing larvae encysted within the host. But in the case of heavy infection, especially where the larva does not encyst within the host, where it works its way out into the water, even a few worms may cause considerable mechanical harm to the host.

In an examination of living material and sections of infected mollusk liver tissue, no infection was found to be so light that the host was unharmed. In

the *Cercaria biflexa* infection of *Physa gyrina* (Fig. 159), where the cyst membrane is moderately heavy, many ceca are uninjured, yet some betray the marks of injury. One such injury is shown in the figure. In this case the cells of the ceca have undergone only a little change. A comparison of this condition with that of *C. microphargnx* infection in *Lymnaea proxima* (Fig. 160) and *C. gracillima* infection in *Physa gyrina* (Fig. 161), shows a comparatively small injury in the former tissue and a severe injury in the latter tissues. Both the latter cases show tissue degeneration. The chemical change in *Lymnaea proxima* is evinced by 1) fatty bodies that have accumulated in some of the cells (*a*), showing as highly refractive inter-cellular inclusions; 2) large vacuoles in the cells (*b*), especially around the nuclei; 3) cytolysis and karyolysis (*c*, *d*), including a sloughing of the tissues in the region of the lumina of the ceca. The condition of *C. gracillima* infection in *Physa gyrina* (Fig. 161) pictures a further degeneration of the tissues. Fatty globules (*b*), are common, usually accumulated as spherules within the wall. Vacuolization (*d*) has progressed to an advanced stage. Cytolysis and karyolysis (*a*, *c*) have gone so far that the outlines of the majority of the cells are indistinct and no difference exists longer between the epithelial and the lymphocytoidal cells. An indefinite, irregular margin marks off the ceca from the interstices in which the cercariae lie. A further change consists in the formation of fibromata (*e*) and granulomata within the degenerating ceca. Finally the epithelium surrounding the entire liver mass has been penetrated by sand granules (*f*), and other foreign bodies have had access to the tissues.

In the infection of *Planorbis trivolvis* with *C. trisolenata* the mass of the worms was about twice that of the liver tissue infected. The tissue was so distended with the parasites that a prick of the needle was sufficient to cause the liver membrane to burst, upon which the rediae and cercariae fairly poured out of the tissue.

The data on the effect of the trematode infection on the molluscan host are significant. No infection is so light that mechanical and chemical injuries are not inflicted. In the heavy infections such as are common to the mollusks of the Bitter Root Valley, the injury is so heavy that it must alter appreciably the life of the host. The mechanical pressure tends to inhibit or increase the functioning of the glandular organs and cramps the tissues within unusual confines. The presence of foreign proteins in close association with the lymph sinuses is sufficient to alter the vital economy of the host. The boring of the worm destroys the tissues locally and in general irritates the mechanism, exposing it to bacterial infection. The secretion of digestive juices by the parasite, and of anti-thrombins and possibly specific poisons, upsets the entire physiological equilibrium of the organism.

PROBLEMS PRESENTED

INTERRELATION OF TREMATODES

In working out new species of organisms, especially from new geographical areas, there are often physiological and morphological facts that are of general significance in the light of previous studies. Relationship is the ultimate problem for all workers in morphology. While light is shed on phylogeny by the discovery of new species, it is futile to expect to found a system of phylogeny on a single species. With these limitations in mind the writer presents some of the more important questions that arise from the study of the trematodes of the mollusks of the Bitter Root Valley.

In the early days cercariae and rediae were considered as different groups of the animal kingdom, and it was not until the life-history studies of Leuckart, La Valette (1855), and Ercolani (1881, 1882) had been published that the genetic relationships of cercariae and parthenitae were established. The germ layers of all generations of trematodes have a similar origin, and important structures of the group present the same problem.

Certain investigators of recent time have come to regard the trematodes as a polyphyletic group. Their conclusion has resulted, perhaps, from their lack of study and consequent inability to recognize the fundamental resemblance of the genital, excretory and nervous systems of the various sub-divisions of the group, especially during the developmental stages.

From more convincing observations Odhner (1907) has concluded that the Monostomata are polyphyletic. He has noted among certain monostomes a structure comparable to the pharyngeal pockets of amphistomes, and among others a primitive acetabulum (1911). In a study of monostome cercariae from the Bitter Root Valley, the similarity of the nervous system and genital cell masses of *Cercaria pellucida* and of those systems in *Gastrothylax gregarius* Looss has been investigated.

Both *Cercaria pellucida* and *Gastrothylax gregarius* show paired brain ganglia closely set together with only slight constriction of the dorsal commissure. In both species the nerve cells lie superficially upon the central nerve ganglion masses. Moreover, relatively large posterior ventral and smaller lateral and dorsal trunks, together with their respective positions, constitute a series of similarities not to be overlooked. The lack of pharyngealis, palatinus, and dorsolateral commissure (Figs. 123, 124) serves to show that the nerve complex of the monostome larva *Cercaria pellucida* is not typically distomate. Its nerve structures are much more readily referred to the Gastrothylax type.

In the second place certain features of the genitalia of *Cercaria pellucida* and Gastrothylax suggest a common ancestry. The median ovary in the subcaudal region; the paired testes lateral to the ovary; the dendritic vitellaria, located in two series, and, finally, the parallel course of the uterus and

the vas efferens to the genital pore far cephalad—all of these show in common a genital system quite distinct from the usual distome types.

The similarity of the nervous and genital complexes of larval monostomes, such as *Cercaria pellucida* and *C. konadensis*, and the amphistome, *Gastrothylax gregarius*, suggest a common origin of certain monostomes and amphistomes.

Among adult distomes there is great variety of structure, yet only in one family, the Schistosomatidae, has the nervous system been fundamentally altered. The structures of the two furcocercous larvae, *Cercaria gracillima* and *C. tuberistoma*, demonstrate their relationship to the Schistosomatidae. The reasons for this belief are these:

The characters which distinguish the apharyngeal furcocercous cercariae are as follows: 1) a forked tail (larval character only); 2) paired groups of salivary-mucin glands (larval); 3) absence of an oral suctorial disc, and in its place 4) an invertible suctorial proboscis; 5) an apharyngeal esophagus, provided with glands in the region usually occupied by a pharynx. The nervous system, more deeply seated, is modified by the degeneration of the posterior laterales during early embryonic development, and the fusion of the posterior dorsales with the posterior ventrales about one-third the body length back from the anterior end (Fig. 150). All of these, except the forked tail and the salivary-mucin glands, are both larval and adult characters. In addition, the larva of *Cercaria gracillima* has several testicular follicles proliferated from the testes-mass at the posterior end of the body.

Certain of the structures of this group also characterize the larvae of other groups of trematodes. For example, *Cercaria cristata* La Val. (1855:23; Taf. II, Fig. K), has a bifid tail and apparently lacks a pharynx, but the fact that it lacks an acetabulum probably separates it from the distome furcocercariae. Among the Gorgorderinae there are apharyngeal cercariae with several testes. However, Ssinitzin (1905:46-51; Taf. I, II) has shown for four Gorgordera species, that the cercariae are characterized in common by 1) a stylet, 2) salivary glands only in the cephalic region of the body, 3) a large glandular excretory vesicle, almost filling the posterior third of the body, and 4) a disproportionately large tail, showing the cystocercous relation of the larvae of the group. Moreover, the nervous system of the Gorgorderinae is typically distomate (Zailer 1914:386).

It may be stated with considerable probability that all of the fundamental organs of the furcocercariae, namely, the apharyngeal esophagus, the multiple testes, and the uniquely modified nervous system, are found in only one family, the Schistosomatidae. All described Schistosomatidae are characterized by the absence of a true oral suctorial disc and by the presence of an invertible oral suctorial pouch. They have no pharynx, but in its stead glands that line the wall of the esophagus. Looss has described the modified nervous system of the family in his study of *Schistosoma haematobium* (1895:

60-68; Taf. II, Fig. 18). It corresponds in detail to the system in *Cercaria gracillima* previously described.

Coupled with these morphological likenesses are the experimental data of Leiper (1915, 1916), Miyuri and Suzuki (1914), and Iturbe and Gonzalez (1917) on Schistosoma life-histories. Leiper has found that the three schistosome species known to infect man, *Schistosoma haematobium*, *S. mansoni*, and *S. japonicum*, give rise to miracidia which have a certain attraction for certain snails in the districts infected. Within the tissues of these snails the miracidia metamorphose into sporocysts, and the second generation sporocysts give rise internally to bifid cercariae with a ventral sucker but without a true pharynx. Furthermore, these cercariae introduced thru the skin of experimental animals, mice and monkeys, give rise to typical unisexual adult schistosomes.

This two-fold evidence favors the view that the furcocercous apharyngeal distome cercariae, including *Cercaria gracillima* and *C. tuberistoma* of the Bitter Root fauna, develop, under proper conditions, into adult schistosomes. One character figured by Leiper for all of his apharyngeal bifid cercariae, yet not used by him as a diagnostic character, is the presence of salivary-mucin glands. On the other hand, one character used by Leiper for cercariae of the group, namely, the absence of a pigment eye, holds for his three species of schistosome larvae, but does not hold for *Cercaria ocellata* La Val., *C. douthitti* Cort, or *C. gracillima*. It has been shown that the eye-spot may be present without pigment (*C. gracillima*). Likewise the failure of Looss to mention an eye-spot for *C. vivax* Sons. (1896:216-223; Figs. 172-174) does not necessarily imply the absence of pigmentless eye-spots in that species.

The relationship of the forked tail apharyngeal distome cercariae will be made much clearer by a consideration of the genital organs. The adult Schistosomas into which the larvae of Leiper develop are characterized by a relatively small number of testicular follicles, 4 to 5 for *S. haematobium*, 6 to 8 for *S. japonicum*, and 8 for *S. mansoni*. On the other hand, the testicle proliferation in *Cercaria gracillima* (Fig. 149) shows twenty-four or twenty-five follicles already differentiated from a posterior germ mass. The large number of testicular follicles has been found to be characteristic of the adult Schistosomatidae of the genera Bilharziella (Kowalewski,1895; 1896), Gigantobilharzia (Odhner, 1912), and Ornithobilharzia (Odhner, 1912). None of these genera and in fact no Schistosomatidae have been reported from North America.

From these considerations it seems probable that *Cercaria gracillima* is the larva of a schistosome genus, such as Bilharziella, Ornithobilharzia or Gigantobilharzia, all of which are bird parasites.

Since the germinal masses of *Cercaria gracillima* are hermaphroditic, and any marked differentiation of the organs does not take place while the larva is outside the definitive host, differentiation of sex in Schistosomatidae takes place in these species comparatively late in their metamorphosis. This view

is in keeping with the studies of Odhner (1912), who points out the fundamental morphological relationship of the hermaphroditic species Liolope and Haplometra to the unisexual Bilharziella, Gigantobilharzia, Ornithobilharzia, and Schistosoma.

The discussion leads to the conclusion that the furcocercous larvae possess in common 1) a bifid tail, 2) a ventral sucker, 3) an oral suctorial pouch which can be inverted, 4) a glandular esophagus without sphincter muscles, 5) paired groups of salivary-mucin glands, four or more to the group, 6) multiple testes, and 7) a specifically modified nervous system. In the light of present knowledge all of these species fall within the limits of the family Schistosomatidae.

Of all the known groups of trematodes the Holostomata have been the group of least genetic study and most erroneous interpretation. On account of their large size the adult holostomes have been known for many years and dozens of species have been described. Nothing, however, has been known of the parthenitae and their development. Without sufficient evidence Brandes (1891:573) has interpreted the sketch of a miracidium of *Strigea* (*Holostomum*) *cornucopiae* Molin (von Linstow,1877, Fig.30) as a metamorphosing tetracotyle. In other words, Brandes concludes that the holostome has a direct development without the intercalation of a parthenogenetic cycle. Ercolani (1881:284-290; Tav. II, Figs. 16-22) has worked out the life-history of *Strigea erratica* (Duj.) from the tetracotyle to the adult form, by infecting *Anas* sp. with *Tetracotyle typica* cysts from the mollusk *Planorbis corneus*. Altho Ercolani found a tetracotyle in a sporocyst (Tav. II, Fig. 18), he interpreted it as the invasion of the tetracotyle into the sporocyst of *Cercaria ocellata* La Val. Ssinitzin (1910:22, 23) has justly criticized Brandes' conclusion of the monogenetic development of holostomes, but in lieu of true holostome evidence in support of the digenetic view he has substituted evidence from *Cercaria plicata*, a peculiar distome larva which he has found to bear certain relationships to the holostomes.

It has been shown in this paper (p. 16) that there are parthenogenetic cycles in *Cercaria flabelliformis*, a typical holostome, and that several generations of rediae are intercalated between the miracidium and the tetracotyle. Thus, there is conclusive proof that the holostome has an alternation of generations, hermaphroditic and parthenogenetic, similar in kind to such alternation in other Digenea.

In spite of the strangely modified suctorial apparatus and posterior genital organs of the holostomes, there seem to be good grounds for believing that they originated from the distomes. They have an acetabulum, and frequently the muscular rudiment of a genital pore just in front of the acetabulum (Fig. 52). On the other hand it is very doubtful if the lappets (Zapfenlappen of Brandes 1892, Taf. 41, Figs. 5-15) bear any homology to the genital pore rudiment. It has been shown, in fact, that the lateral lappets in *Cercaria flabelliformis* arise from a pair of oval suctorial grooves (Fig. 41), and that in

Tetracotyle pipientis (Fig. 47), where these grooves remain rudimentary, no lateral lappets develop.

As von Linstow (1877:189) pointed out, species characters in Strigea (Holostomum) have been treated very superficially, since the group members are not readily distinguished by external markings and the internal anatomy is difficult to interpret. Yet the writer has found that even in the early larva the points of differentiation are well marked. The parthenogenetic egg of the holostome developing into the cercaria is at the time of maturation structurally different from the ova developing into a redia. Thus the actual phylogenetic history of the group is hidden by its precocity and the developmental stages of the holostome show only in telescopic fashion the actual ancestral history.

Extraordinary nerve modification in the holostomes (Fig. 53) is related directly to the modification of the muscle complex. This modification consists usually in the degeneration of the posterior dorsales and laterales, and a relative increase in size and importance of the posterior ventrales. The other systems of the holostomes, especially the genital and excretory organs, are equally highly modified and equally well formed in the larva. Ssinitzin (1910, 1911) has suggested that the change in the genital pore from the preacetabular position to the posterior ventral extremity has come about thru the formation of a new opening rather than thru a shifting of the old preacetabular pore. The original pore is still present in the larvae, altho in most cases there is no clue to its former connection or function. The extent of these changes indicates a long period of gradual adjustment to a modifying environment.

The study of the cercariae of the various groups of the Digenea not only serves to supplement relationship studies in adult hermaphroditic generations of trematodes, but also brings out structural relationships very considerably if not entirely hidden in the adult. The most constant of all the systems in the group Digenea is the nervous system. Any marked modification from the characteristic distomate type is indicative of a considerable period of divergent growth.

The fundamental systems of the hermaphroditic generation of the trematode are deep seated; they are well formed in the cercaria, and little significant differentiation takes place during metamorphosis.

RELATION OF TREMATODES TO OTHER GROUPS

Among the early systematists Trematoda were classified with the Hirudinea because of the common superficial resemblance of the two groups. Even as late as 1871 Schmarda separated the Trematoda from the Turbellaria and Cestoda, and placed them with the Hirudinea in the Cotylidea. Balfour (1881:316, 317) considered a direct relationship of all Metazoa above Coelenterata entirely unsatisfactory and conceived the idea of referring them all back to the trochophore larva which possessed radial symmetry. In his

monograph on *Amphistomum subclavatum*, Looss (1892:156, 157) compared the proliferation of the germ-balls from the body wall of the parthenita to the production of eggs and spermatozoa in the marine polychaetes, and suggested that other embryonic structures of the trematode were comparable to annelid structures, so that they might be considered of phylogenetic value. Recently Ssinitzin (1911:86) has spoken of the resemblance of the Trematoda to Arthropoda and Trochelminthes, in view of the absence of any ciliary integument, in place of which, he says, the cuticula and the external skeleton develop.

During this time the theory of the common descent of the Trematoda, Cestoda and Turbellaria has been gaining ground, not because they are all "flatworms," as Ssinitzin insists, but on the homologies of the genital, excretory and nervous systems. The observations of Leuckart (1886:140), Schulze (1853:178-195), and Schneider (1864:590-597) all support this view, while Leuckart even saw the analogy between the gutless sporocyst and the Acoela. Lang (1884:669) showed that the nervous system of the Trematoda and Turbellaria was homologous.

With the work of Haswell on Temnocephala (1888) the close affinities of the Trematoda and the Turbellaria became evident. In this group the excretory system, the three anterior and posterior nerve trunks, the anterior mouth, and the dorsal pigment eyes—all these bridged the way for the acceptance of the thesis that the Trematoda and the Turbellaria have a common ancestry.

The study of the parthenogenetic generations of the Digenea, to which this paper is devoted, stands in support of this thesis and contributes the following facts towards its further acceptance.

1. The body cavity of the hermaphroditic generations of trematodes and of Turbellaria is filled with differentiated mesenchyme and connective tissue. In the parthenitae the parenchyma is confined to the body wall because it is less differentiated.

2. Both Trematoda and Turbellaria are typically flat, with a pronounced bilateral symmetry. The cylindrical appearance of the parthenitae is a secondary modification due to parasitism.

3. The epidermis of Trematoda and Turbellaria consists of a single layer of cells. In the sporocyst larva, the miracidium, and in the Turbellaria, the epithelial layer is ciliated. In the rediae and in the cercariae the layer is usually sloughed off before maturity and in its place the basement membrane of mesodermal origin, serves as the integument.

4. The nervous system of the Monogenea, the Digenea, and the Turbellaria is reducible to a common type. Two brain ganglia with a transverse commissure, three anterior pairs of nerve trunks, and three anterior pairs of nerve trunks—these are common to all three groups. Moreover, the pigment eyespots of the Turbellaria, Monogenea, and Digenea are not only homologous, but practically identical in detail (Hesse 1897; and page 52 this paper). In

each case one or more ganglion cells fill the optic cup. In each it can be traced to the brain center. Parasitism has caused the pigment eye to degenerate in most adult Digenea. Even in the cercariae it is pigmented only in certain species; other species have lost all traces of pigment, but the optic nerve is still present and can be traced to the brain center. In many cases it has been lost, even in the cercariae. Eye-spots are common in miracidia, but are lost on metamorphosis into the sporocyst. There are no records of eyes in rediae.

5. The digestive tract of the cercariae and the adult hermaphroditic generations of trematodes is usually triclad. In the redia the gut is rhabdocoel; there is a pharynx and salivary glands have been described (Ssinitzin, 1911, and pp. 63, this paper). In the miracidium, there is an indication of a rhabdocoel gut and salivary glands (Looss, 1892; Miyuri and Suzuki, 1914), altho these are usually lost in the adult. In the Turbellaria the gut is triclad, polyclad, rhabdocoel or acoel. The pharynx is ordinarily present and salivary glands are common.

6. The excretory system in the two groups is at first a single pair of protonephridia. This condition is found in miracidia, rediae, cercariae and Turbellaria alike. The capillaries, whether in the larva or adult, end in flame cells.

7. The genital system was one of the first in which investigators recognized the relationship between the Trematoda and the Turbellaria. The hermaphroditic condition in the hermaphroditic generation of the Trematoda is strikingly similar to that of the Turbellaria, with the common genital atrium in all groups except Acoela. Parthenogenesis in parthenitae is the result of the great change in environment of these cycles.

Thus the main trend of investigation has come to support the common origin of the Trematoda and the Turbellaria.

LIFE CYCLE OF THE DIGENETIC TREMATODES

The life-history of the trematode of the order Digenea consists not in an alternation of sexual and asexual generations, but rather of successive sexual generations which are parthenogenetic and hermaphroditic.

A problem which has arisen in connection with the genitalia of the Digenea is the significance of Laurer's canal. Looss (1893a) considers it homologous to the uterus of Cestoda, while Goto (1893) believes it to be the homolog of the blind vagina of Amphilina and the genito-intestinal canal of Monogenea. According to Lühe (1909) a Laurer's canal is present in Monostomes, and in some groups of the distomes, including Plagiorchiidae and Echinostomidae. It has not been recorded for holostomes or Schistosomatidae. Except for the Echinostomid cercariae, a Laurer's canal has been found in all cercariae of the groups studied by the writer, where the adult trematode has the canal. Absence of the canal in Echinostomid cercariae can be explained on the basis of late development of the genital organs in this family. On the other

hand, no Laurer's canal has been found in the groups where no canal is present in the adult. Students of cercariae have not as a rule recorded the canal in trematode larvae. Ssinitzin (1905, Figs. 62, 67, 74) has found it in the three xiphidiocercariae, *Cercaria gibba* de Fil., *C. prima*, and *C. secunda*. The constant development of this organ in the several groups described in this paper shows that the canal originally had an important place in the genital processes of the Digenea.

The pronounced difference in structure between parthenogenetic ova which develop into rediae and those which develop into cercariae has been discussed (p. 18). This difference has been found to bear no relation to the phenomenon of maturation, since the chromosome count in the mature cells is the same, whether redia or cercaria is to be produced. In fact, it seems probable that the differentiation occurs before maturation. It is significant that the ova which develop into redia are comparatively simple while the ova which develop into cercariae are extremely complex. In this connection it has been observed that embryos developing from germ-balls produced from ova free in the body cavity produce daughter rediae. The maturing ova from the germinal epithelium lodged in the body wall of the parthenita develop either into rediae or cercariae.

In his experiments on planarians Child (1915) has shown that starvation and fragmentation (fission) secure a rejuvenescence for the individual. The less differentiated individual is on the whole the younger one. From the present study on the life-history of trematodes there is justification for the belief that the undifferentiated eggs produce daughter parthenitae because they are simple, i.e., younger, while the more highly differentiated eggs grow into cercariae because they are physiologically old. Interpreted in this light, the parthenitic individuals of the Digenea are physiologically younger than the cercariae and the adult hermaphroditic forms because their structure is simpler. They have sacrificed complexity of structure to meet the needs of the parasitic life, and in so doing have become remarkably rejuvenated. In two species, *Cercaria diaphana* and *C. micropharynx* extreme simplicity has been assumed in the sporocyst, for the germ-balls develop from any cell of the body wall.

The writer believes that the ability of the parthenita to reproduce daughter rediae or sporocysts for two or more generations rests on the simplicity of the ovum and the relative simplicity of the parthenita, especially as regards the undifferentiated mesoderm cells. If this rejuvenation can be continued indefinitely, the parthenogenetic generations can also continue indefinitely without the intercalation of the hermaphroditic cycle.

Child (1915:407) has stated that "in many cases parthenogenetic eggs are apparently less highly differentiated morphologically, and younger physiologically, than zygogenic eggs of the same species." The present study makes it necessary to add that in cases where the parthenogenetic eggs may develop into parthenitae or cercariae, the eggs which develop into the former

individuals are apparently less highly differentiated morphologically and younger physiologically than those which develop into cercariae.

Finally the present study causes the writer to support the view that the hermaphroditic phase of the life cycle of the Digenea is more closely related to the ancestral group than the parthenita, and that the simplicity of the parthenita has been assumed secondarily. This conclusion is based on the evidence that the original type was a highly complex Platyhelminth with ciliary integument and eye-spots, characters found only in the miracidium. The modification of the parthenita has come about as the direct result of parasitism. It has lost its mesenchymatous matrix, its excretory tract has been extraordinarily modified, and its germ cells have become uniquely simple. The nervous system of the redia has been simplified while the sporocyst lacks a nervous system entirely. In the sporocyst even the muscle cells have remained undifferentiated. Thus complexity in the hermaphroditic generation of Digenea is an index of the unmodified condition of the group most early related to the prototype.

SUMMARY

1. Trematode infection of mollusks of the Bitter Root Valley, Montana, is heavy.

2. The history of the germ cells of the sporocyst and redia show them to arise parthenogenetically.

3. Parthenitae and adult hermaphoditic trematodes are comparable individuals: likewise their germ cells can be referred to a common type of germinal epithelium.

4. The integument of trematodes is mesodermal in origin.

5. The fundamental systems of the adult hermaphroditic trematode are well developed in the cercaria.

6. The excretory, genital and nervous systems of the cercaria may be used to show the natural relationships of the larvae.

7. Holostomes, like distomes, monostomes and amphistomes, have an alternation of hermaphroditic and parthenogenetic generations.

8. Holostomes are probably of distome origin.

9. Parthenitae are well adapted to their parasitic life because their structure is simple, in consequence of which they have become physiologically young.

SPECIES DESCRIBED IN THIS PAPER.

MONOSTOMATA
- *Cercaria pellucida* Faust 1917
- *Cercaria konadensis* Faust 1917

HOLOSTOMATA
- *Cercaria flabelliformis* Faust 1917
- *Tetracotyle pipientis* nov. spec.
- *Cercaria ptychocheilus* Faust 1917

DISTOMATA

Xiphidiocercariae
- *Cercaria crenata* Faust 1917
- *Cercaria glandulosa* Faust 1917
- *Cercaria diaphana* Faust 1917
- *Cercaria dendritica* Faust 1917
- *Cercaria micropharynx* Faust 1917
- *Cercaria racemosa* Faust 1917

Echinostome Cercariae
- *Cercaria trisolenata* Faust 1917
- *Cercaria biflexa* Faust 1917

Furcocercariae
- *Cercaria gracillima* Faust 1917
- *Cercaria tuberistoma* Faust 1917

BIBLIOGRAPHY

ANDRÉ, J.
1910. Zur Morphologie des Nervensystems von Polystomum integerrimum Froel. Zeit. wiss. Zool., 95:191-220; 13 textfigs.

BALFOUR, F. M.
1881. A Treatise on Comparative Embryology, vol. II. London, 655 pp.

BARKER, F. D., and LAUGHLIN, J. W.
1911. A New Species of Trematode from the Muskrat, *Fiber zibethicus*. Trans. Amer. Micr. Soc., 30:261-274; 1 pl.

BETTENDORF, H.
1897. Ueber Musculatur und Sinneszellen der Trematoden. Zool. Jahrb., Anat., 10:307-357; 5 Taf.

BLANCHARD, E.
1847. Recherches sur l'organization des vers. Ann. sci. nat., zool. (3) 8:271-341; 5 pl.

BLOCHMANN, T.
1896. Die Epithelfrage bei Cestoden und Trematoden. Sep., 6ten Vers. deutschen Zool. Ges. zu Bonn. Hamburg. 12 pp., 2 Taf.

BOVAIRD, D., and CECIL, R. L.
1914. Schistosomiasis japonica; a Clinical and Pathological Study of Two Cases. Amer. Jour. Med. Sci., 148:187-206; 3 figs.

BRANDES, G.
1891. Die Familie der Holostomiden. Zool. Jahrb., Syst., 5:547-604; 3 Taf.
1892. Zum feineren Bau der Trematoden. Zeit. wiss. Zool., 53:558-577; 1 Taf.

BRAUN, M.
1893. Vermes. Trematodes. Bronn's Thierreich, IV, 1A. Leipzig. pp. 306-925; 27 pl.
1901. Zur Revision der Trematoden der Vögel. I. Centralbl. Bakt. u. Parasit., Orig. (I) 29:560-568.
1901a. Zur Revision der Trematoden der Vögel, II. Centralbl. Bakt. u. Parasit., Orig. (I) 29:895-897, 941-948.

BROWN, A. W.
1899. On *Tetracotyle petromyzontis*, a parasite of the Brain of Ammocetes. Quar. Jour. Micr. Sci., 41:489-498; 1 pl.

CARY, L. R.
1909. The Life History of Diplodiscus temperatus Stafford. With Especial Reference to the Development of the Parthenogenetic Eggs. Zool. Jahrb., Anat., 28:595-659; 4 pl.

CHILD, C. M.
1915. Senescence and Rejuvenescence. Chicago. 481 pp.

COE, W. R.
1896. Notizen über den Bau des Embryos von Distomum hepaticum. Zool. Jahrb. Anat., 9:561-570; 1 Taf.

CORT, W. W.
1914. Larval Trematodes from North American Fresh-Water Snails. Jour. Parasit., 1:64-84; 13 Figs.
1915. Some North American Larval Trematodes. Ill. Biol. Monogr., 1:447-532; 8 pl.

DIETZ, E.
1910. Die Echinostomen der Vögel. Zool. Jahrb., Suppl., 12:265-512; 6 Taf.

ERCOLANI, G.
1881. Dell' adattemento della specie all' ambiente. Nuove ricerche sulla storia genetica dei Trematodi. I. Mem. r. Acc. Ist. Bologna., (4) 2:239-334; 3 Tav.

1882. Dell' adattemento della specie all' ambiente. Nuove ricerche sulla storia genetica dei Trematodi. II. Mem. r. Acc. Ist. Bologna., (4) 3:43-111; 3 Tav.

FANTHAM, H. B.

1916. The Animal Parasites of Man. London. 900 pp. 415 Figs.

FAUST, E. C.

1917. Notes on the Cercariae of the Bitter Root Valley, Montana. Jour. Parasit., 3:105-123; 1 pl.

DE FILIPPI, Ph.

1857. Troisième mémoire pour servir à l'histoire génétique des Trématodes. Mém. Acad. Sci. Turin., (2) 18:1-34; 3 pl.

FISCHER, P. M.

1883. Ueber den Bau von Opisthotrema cochleare nov. genus, nov. spec. Zeit. wiss. Zool., 40:1-42; 1 Taf.

GAFFRON, E.

1884. Zum Nervensystem der Trematoden. Zool. Beitr., 1:109-115; 1 Taf.

LA VALETTE ST. GEORGE.

1855. Symbolae ad Trematodum Evolutionis Historiam. Berolini 40 pp., 2 Taf.

GOTO, S.

1893. Der Laurer'sche Kanal und die Scheide. Centralbl. Bakt. u. Parasit., Orig. (I) 14:797-801; 4 Figs.

1894. Studies on the Ectoparasitic Trematodes of Japan. Jour. Coll. Sci. Imp. Univ. Japan., (1) 8:1-273; 27 pl.

HASWELL, W. A.

1888. On Temnocephala, an Aberrant Monogenetic Trematode. Quart. Jour. Micr. Sci., 28:279-302; 3 pl.

1903. On Two Remarkable Sporocysts Occurring in Mytilus latus on the Coast of New Zealand. Proc. Linn. Soc. N. S. Wales, 27:494-515; 2 pl.

HAUSMANN, L.

1897. Über Trematoden der Süsswasserfische. Rev. suisse zool., 5:1-42; 1 Taf.

HESSE, R.

1897. Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. II. Die Augen der Platyhelminthen. Zeit. wiss. Zool., 62:527-582; 2 Taf.

HOFMANN, K.

1899. Beiträge zur Kenntnis der Entwicklung von Distomum leptostomum Olsson. Zool Jahrb., Syst., 12:174-204; 2 Taf.

ITURBE, J. and GONZÁLEZ, E.

1917. The intermediate host of *Schistosomum mansoni* in Venezuela. Natl. Acad. Med. Caracas. Sep. 7 pp., 2 pl.

JÄGERSKIÖLD, L. A.

1891. Ueber den Bau des Ogmogaster plicatus (Creplin). Kgl. svenska Vetensk. Akad. Handl., (7) 24:1-32; 2 Taf.

JOHNSTON, S. J.

1904. Contributions to a Knowledge of Australian Entozoa. III. On Some Species of Holostomidae from Australian Birds. Proc. Linn. Soc. N. S. Wales, 29:108-116; 3 pl.

1916. On the Trematodes of Australian Birds. Jour. Proc. R. Soc. N. S. Wales, 50: 187-261; 11 pl.

JUEL, H.

1889. Beiträge zur Anatomie der Trematodengattung Apoblema (Dujard.). Kgl. Sv. vetensk. Akad. Handl., (4) 15:1-46; 1 Taf.

KATSURADA, F.

1914. Schistosomiasis japonica. Centralbl. Bakt. u. Parasit., Orig. (I) 72:383-379; 2 Taf.

KOWALEWSKI, M.
1895. Studya helminthologiczne. III. Bilharzia polonica, n. sp. Rozpraw Wydz., mat.-przyr. Akad. Umiejet. Krakowie, (1) 31:1-30; 2 pl.
1896. Studya helminthologiczne. IV. Bilharzia polonica, n. sp. Rozpraw Wydz., mat.-przyr. Akad. Umiejet. Krakowie, (1) 30:1-12.
1896a. Études Helminthologiques. IV. Amendements et Suppléments au travail de l'auteur sur le Bilharzia polonica sp. nov. Bull. acad. sci. Cracovie, 1896:146-148.
LANG, A.
1880. Untersuchungen zur vergleichenden Anatomie und Histologie des Nervensystems der Platyhelminthen. II. Ueber das Nervensystem der Trematoden. Mitth. Zool. Sta. Neapel, 2:28-52; 3 Taf.
1884. Die Polycladiden des Golfes von Neapel. Fauna u. Flora von Neapel, (2) 11: 1-688; 39 pl.
LANKESTER, E. R.
1901. A Treatise on Zoölogy. IV. The Platyhelmia, Mesozoa, and Nemertini. London. 204 pp.
LA RUE, G. R.
1917. Two New Larval Trematodes from Thamnophis marciana and Thamnophis eques. Occasional Papers Mus. Zool. Univ. Mich., No. 35; 14 pp., 1 pl.
LEBOUR, MARIE V.
1907. Larval Trematodes of the Northumberland Coast. Trans. Nat. Hist. Soc. Northumberland, n.s., 1:437-454; 5 pl.
LEIDY, J.
1877. On Flukes infesting Mollusks. Proc. Acad. Nat. Sci. Phila., 29:200-202.
1890. Notices on Entozoa. Proc. Acad. Nat. Sci. Phila., 42:410-418.
1904. Researches in Helminthology and Parasitology. Smiths. Inst. Misc. Coll. Vol. 46, 281 pp.
LEIPER, R. T.
1915. Report on the Results of the Bilharzia Mission in Egypt, 1915. III. Jour. R. Army Med. Corps, 25:253-267; 15 Figs.
1916. On the Relation between the Terminal-Spined and the Lateral-Spined Eggs of Bilharzia. Brit. Med. Jour., 1916, 1:411.
LEIPER, R. T., and ATKINSON, E. L.
1915. Observations on the Spread of Asiatic Schistosomiasis. Brit. Med. Jour., 1915, 1:201-203; 1 pl.
LEJTENYI, TH.
1881. Ueber den Bau des Gastrodiscus polymastos Leuck. Abhandl. Senkenberg. naturf. Ges. Frankfurt, 12:125-146; 3 Taf.
LEUCKART, R.
1863. Die Menschlichen Parasiten. Leipzig. 766 pp.
1886. Die Parasiten der Menschen. 2 Aufl. 1, Trematodes. Leipzig u. Heidelb. 534 pp.
LEYDIG, FR.
1853. Helminthologische Notizen. Zeit. wiss. Zool., 4:382-384.
LINDNER, E.
1914. Ueber die Spermatogenese von Schistosomum haematobium Bilh. (Bilharzia haematobia Cobb.), mit besonderer Berücksichtigung der Geschlechtschromosomen. Arch. Zellforsch., 12:516-538; 2 Taf.
LINSTOW, O.
1877. Enthelminthologica. Arch. Naturgesch., (1) 43:173-198; 3 Taf.
LOOSS, A.
1885. Beiträge zur Kenntnis der Trematoden. Zeit. wiss. Zool., 41:390-446; 1 Taf.
1892. Ueber Amphistomum subclavatum Rud. Leuckart's Festschr., 142-167; 2 Taf.

1893. Zur Frage nach der Natur des Körperparenchyms bei den Trematoden. Ber. K. Sachs. Ges. wiss., mat.-phys. Cl., Sitz. 9 Jan. 1893, 10-34.

1893a. Ist der Laurer'sche Kanal der Trematoden eine Vagina? Centralbl. Bakt. u. Parasit., Orig. (I) 13:808-819; 4 figs.

1894. Die Distomen unserer Fische und Frösche. Bibl. Zool., 16:1-296; 9 Taf.

1895. Zur Anatomie und Histologie von Bilharzia haematobia (Cobbold). Arch. mikr. Anat., 46:1-108; 3 Taf.

1896. Recherches sur la faune parasitaire de l'Égypte. Première partie. Mém. l'institute Égyptien, 3:1-252; 16 pl.

1899. Weitere Beiträge zur Kenntnis der Trematoden-Fauna Aegyptiens. Zool. Jahrb., Syst., 12:521-784; 9 Taf.

1913. Die Bilharziakrankheit. Handbuch der pathogenen Mikro-organismen, 2 Aufl., Sep. 22 pp.

LORTET, L., ET VIALLETON, L.

1894. Étude sur le Bilharzia et la Bilharziose. Ann. Univ. Lyon, (1) 9, 124 pp., 8 pl. Cited after Looss 1895.

LÜHE, M.

1909. Parasitische Plattwürmer. I. Trematodes. Süsswasserfauna Deutschlands Heft 17. Jena. 218 pp.

LUTZ, A.

1916. Observaçoes sobre a evolucão do Schistosomum mansoni. Nota previa. Brazil Medico, 30:385-387.

MATHEWS, A. P.

1915. Physiological Chemistry. New York. 1040 pp.

MINOT, C. S.

1897. Cephalic Homologies. A Contribution to the Determination of the Ancestry of the Vertebrates. Amer. Nat., 31:927-943.

MIYAIRI, K. UND SUZUKI, M.

1914. Der Zwischenwirt des Schistosomum japonicum Kat. Mitt. med. Fakult. Univ. Kyushu, Fukuoka. 1:187-197; 2 Taf.

MONTGOMERY, R. E.

1906, 1906a. Observations on Bilharziosis among Animals in India. Jour. Trop. Vet. Sci., (1) 1:1-32, (1) 2:1-37; 4 pl.

MONTICELLI, Fr. Sav.

1892. Cotylogaster Michaelis nov. gen., nov. spec. Leuckart's Festschr., pp. 164-214; 2 Tav.

1914. Ricerche sulla Cercaria setifera di Joh. Müller. Ann. Mus. zool. Univ. Napoli, (4) 4:1-49; 5 Tav.

MOULINIÉ, J. J.

1856. De la Reproduction chez les Trematodes Endoparasites. Mém. de l'Inst. Genevois, 3:1-280; 6 pl.

NITZSCH, CH. L.

1807. Seltsame Lebens- und Todesart eines bisher unbekannten Wasserthierchens. Kilian, Georgia. 257-262; 281-286. Cited after Braun 1893.

1816. Beitrag zur Infusorien-kunde der Naturbeschreibung der Zerkarien und Bazillarien. Neue Schrift. Nat. Ges. Halle (1) 3; 1 Taf. Reviewed in Isis, 1818:728

NORDMANN, A. v.

1832. Mikrographische Beiträge. I. Berlin. 118 pp., 10 Taf.

ODHNER, T.

1907. Zur Anatomie der Didymozoen: ein getrenntgeschlechtlicher Trematode mit rudimentären Hermaphroditismus. Zool. Studien Tullberg, 1907:309-342; 1 Taf.

1910. Gigantobilharzia acotylea, n.g., n.sp., ein mit den Bilharzien verwandter Blutparasit von enormer Lange. Zool. Anz., 35:380-385; 5 Figs.

1911. Zum natürlichen System der digenen Trematoden. 1. Zool. Anz., 37:181-191.
1912. Zum natürlichen System der digenen Trematoden. V. Zool. Anz., 41:54-71; 7 Figs.

PAGENSTECHER, H. A.
1857. Trematodenlarven und Trematoden. Heidelb. 56 pp., 6 Taf.

PARONA, C., E ARIOLA, V.
1896. Bilharzia Kowalewskii n. sp. nel Larus melanocephalus. Boll. Mus. Zool. e Anat. Comp. Univ. Genova, 45:1-3.

POIRIER, J.
1886. Trématodes nouveaux ou peu connus. Bull. Soc. philomath. Paris. Seance du 28 Nov. 1885. 21 pp. 4 pl.

PRATT, H. S.
1909. The Cuticula and Subcuticula of the Trematodes and Cestodes. Amer. Nat., 43:705-729; 12 Figs.

RETTGER, L. J.
1897. Some Additions to our Knowledge of the Anatomy and Embryology of the Holostomidae. Proc. Ind. Acad. Sci., 1896:224, 225.

REUSS, H.
1903. Beobachtungen an der Sporocyst und Cercaria des Distomum duplicatum. Zeit. wiss. Zool., 74:458-477; 1 Taf.

ROSSBACH, E.
1906. Beiträge zur Anatomie und Entwicklungsgeschichte der Redien. Zeit. wiss Zool., 84:361-445; 4 Taf.

ROSSETER, T. B.
1909. On Holostomum excisum (Linstow, 1906) and the Development of the Tetracotyliform Larva to a Holostomum sp. Jour. Quek. Micr. Club, (2) 10:385-392; 1 pl.

RUDOLPHI, C. A.
1819. Entozoorum Synopsis. Berlin. 812 pp.

SCHAUINSLAND, H.
1883. Beiträge zur Kenntnis der Embryonalentwicklung der Trematoden. Jenai. Zeit. Naturwiss., 16:465-527; 3 Taf.

SCHMARDA, L. K.
1871. Zoologie. Vol. I. Wien. 372 pp.

SCHNEIDER, A.
1864. Ueber die Muskeln der Würmer und ihre Bedeutung für das System. Arch. Anat. Physiol., 1864:590-597.

SCHULZE, M.
1853. Zoölogische Skizzen. Zeit. wiss. Zool., 4:178-195.

SCHWARZE, W.
1886. Die postembryonale Entwicklung der Trematoden. Zeit. wiss. Zool., 43:41-86; 1 Taf.

SIEBOLD, TH. V.
1835. Helminthologische Beiträge. I. Arch. Naturgesch., (1) 1:45-83; 1 Taf.

SSINITZIN, D. TH.
1905. Distomes des poissons et des grenouilles des environs de Varsovie. Materiaux pour l'histoire naturelle des Trématodes Mém. soc. nat. Varsovie. Biol., 15:1-210, 6 pl. Russian.
1910. Studien über die Phylogenie der Trematoden. Biol. Zeit., 1:1-63; 2 Taf.
1911. La génération parthénogénétique des Trématodes et sa descendance dans les mollusques de la Mer Noire. Mém. Acad. Sci. St. Petersbourg, (8) 30:1-127; 6 pl. Russian.

Steenstrup, J. J. S.
1842. Ueber den Generationswechsel oder die Fortpflanzung und Entwicklung durch abwechselnde Generationen. Copenh. 60 pp.
Stiles, Ch. W., and Hassall, A.
1908. Index Catalog of Medical and Veterinary Zoölogy. Trematoda and Trematode Diseases. U. S. Hyg. Lab. Bull. 37. 401 pp.
Surface, F. M.
1907. The Early Development of the Polyclad, Planocera inquilina. Proc. Acad. Nat. Sci. Phila., 59:514-559; 6 pl.
Tennent, D. H.
1906. A Study of the Life History of Bucephalus haimaenus: a Parasite of the Oyster. Quart. Jour. Micr. Sci., n.s., 49:99-133; 2 pl.
Thomas, A. P.
1883. Life History of the Liver Fluke. Quart. Jour. Micr. Sci., 23:99-133; 2 pl.
Thoss, E.
1897. Ueber den Bau von Holostomum cucullus nov. spec. Leipzig. 66 pp., 2 Taf.
Ward, H. B.
1909. Fasciolopsis buskii, F. Rathouisi, and Related Species in China. Trans. Amer. Micr. Soc., 29:5-16; 2 pl.
1916. Notes on Two Free-Living Larval Trematodes from North America. Jour. Parasit., 3:10-20; 1 pl.
Wright, S.
1912. Notes on the Anatomy of Microphallus opacus. Trans. Amer. Micr. Soc., 31: 167-176; 2 pl.
Zailer, O.
1914. Zur Kenntnis der Anatomie der Muskulatur und des Nervensystem der Trematoden. Zool. Anz., 44:385-396; 3 Figs.

EXPLANATION OF PLATES

Abbreviations

ad	anterior dorsalis nerve	ne	nerrve ending
al	anterior lateralis nerve	np	nervus palatinus
as	anterior sensory field	nph	pharyngealis nerve
av	anterior ventralis nerve	ns	subesophageal commissure
b, bc	genital atrium	nt	nerve trunk
bl	bursa glands	o	ovum
br	cerebral ganglion	od	oviduct
c, ce	cecum	on	oral nerve ring
ca	caudal pocket	op	optic nerve cell
ceg	cercaria germ-ball	opc	optic cup
cg	caudal gland cells	opn	optic nerve
cr	cirrus pouch	or	oral sucker
cs	collar spines	ot	ootype
d, dl	salivary gland duct	ov	ovary
dc	dorsal commissure	p	pharynx
dlc	dorsolateral commissure	pa	parenchyma
dp	profundus of dorsalis nerve	pb	polar body
ds	superficialis of dorsalis nerve	pc	preacetabular commissure
e	epithelium	pd	posterior dorsalis nerve
ec	ectoderm	pe	preoral sense endings
eg	excretory granules	pg	primitive genital pore
eb	evertible prepharynx	pgl	locomotor pocket glands
ep	excretory pore	pl	posterior lateralis nerve
es	esophagus	po	postacetabular commissure
et	excretory tube	pv	posterior ventralis nerve
ev	excretory vesicle	pvc	postero-ventrolateralis commissure
ex	excretory tubule	pvi	postero-ventral intermedius nerve
fc	flame cell	r	rhabdocoel gut
g	genital pore, birth pore	rm	ramus muscularis of the lateralis nerve
gb	germ-ball	rp	ramus palpalis of the lateralis nerve
glc	cystogenous cell	sg	salivary gland cell
i	intermedius nerve	sp	acetabular spine
igl	digestive gland	st	stylet
l	longitudinal muscle cell	t	basement membrane
lc	Laurer's canal	te, $t_{1,2}$	testis
le	lateral eye	tr	transverse muscle fiber
lg	localized germinal epithelium	u	uterus
lp	posterior locomotor pocket	v	vagina
ls	lateral suctorial groove	vd	vas deferens
m	myoblast	ve	vas efferens
me	median eye-spot	vf	vitelline follicles
mp	musculus preoralis	vi	vitelline duct
n, nc	nerve cell	vs	acetabulum

The lines in figures 6, 26, 51, 146, 147 have a value of 0.5mm; in figures 5, 7, 13-17, 19-20, 27-29, 31-34, 36, 37, 44-46,54, 56, 57, 61, 68-75, 77, 82, 83, 89, 91, 92, 97-99, 101, 102, 104, 107, 108, 111-113, 118, 119, 121-133, 136, 138, 140, 141, 145, 150-154, a value of 0.01 mm; in all other figures, a value of 0.05 mm.

PLATE I

DESCRIPTION OF PLATE

Figs. 1-3.—*Cercaria pellucida*; sketches of progressive stages of pigmentation; dorsal view, showing two lateral eye-spots and one median spot. × 100.

Fig. 4.—*Cercaria pellucida*; dorsal view, somewhat contracted. × 100.

Fig. 5.—*Cercaria pellucida*; anterior tip, figuring details of pigmentation and contents of the excretory tube. × 330.

Fig. 6.—*Cercaria pellucida*; redia, characterized by extensive rhabdocoel gut and spinous prepharynx. × 34.

Fig. 7.—*Cercaria pellucida*; detail of the spinous prepharynx of the redia. × 540.

Fig. 8.—*Cercaria pellucida*; young redia; precocious development of the cercariae before the redia is mature. × 38.

Figs. 9-11.—*Cercaria pellucida*; three stages in encystment. × 38.

Fig. 12.—Young *Cercaria pellucida*; origin of posterior locomotor pockets within the caudal pocket. × 170.

Fig. 13.—*Cercaria pellucida*; transverse section thru the middle of the body. × 330.

Fig. 14.—*Cercaria pellucida*; detail of cystogenous gland cells in the region of the lateral eye-spot. × 330.

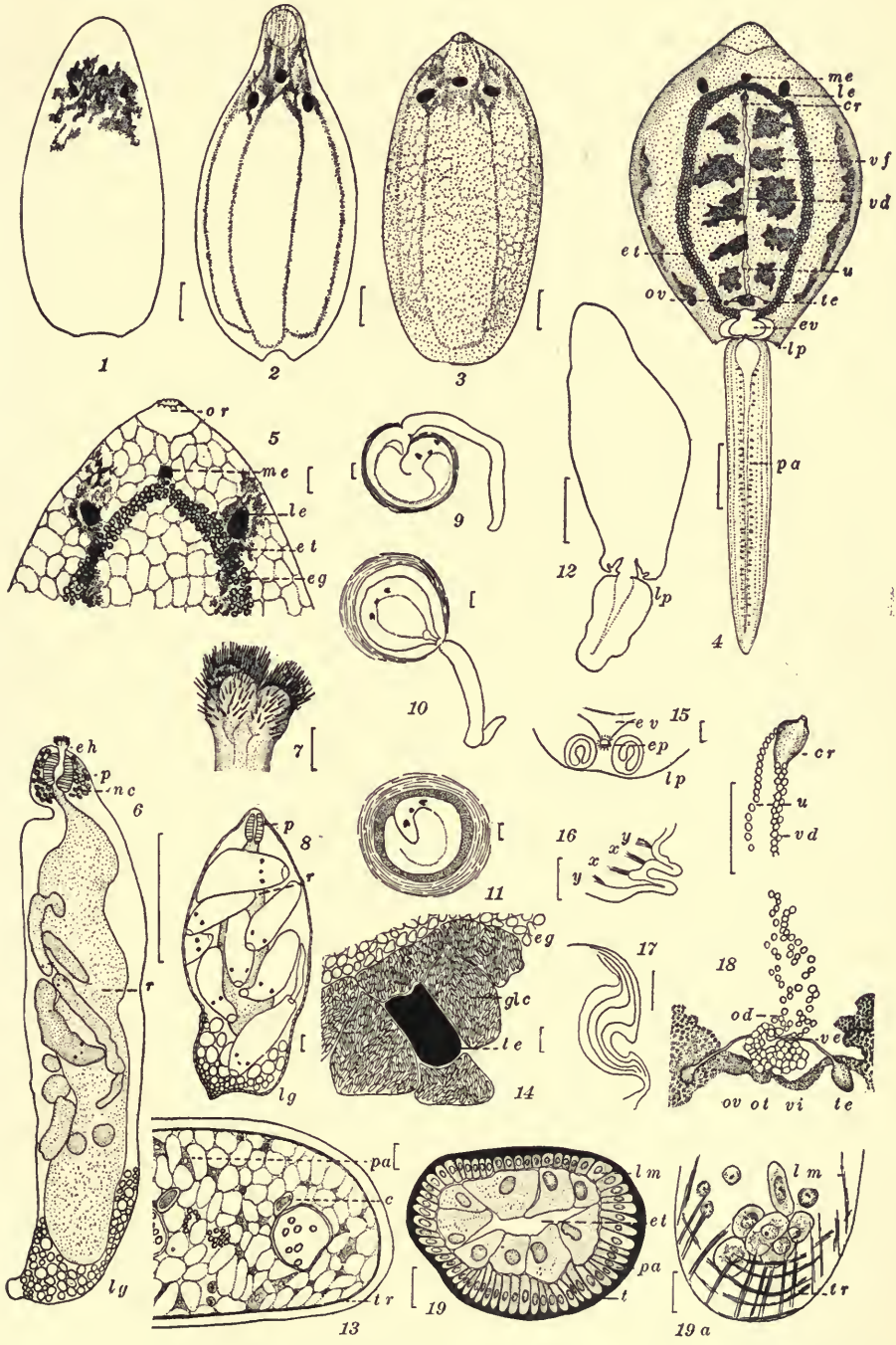
Fig. 15.—*Cercaria pellucida*; contracted excretory bladder and posterior locomotor pockets. × 238.

Figs. 16, 17.—*Cercaria pellucida*; details of the posterior locomotor pocket; Fig. 16, contracted; Fig. 17, relaxed; *xx*, retractor muscles; *yy*, reflexor muscles. × 540.

Fig. 18.—The genitalia of *Cercaria pellucida*; regions of ootype and metraterm. × 238.

Fig. 19.—*Cercaria pellucida*; transverse section thru tail, indicating arrangement of ordinary parenchyma cells. × 540.

Fig. 19a.—*Cercaria pellucida*; oblique section thru tail, indicating arrangement of muscle fibers. × 540.



FAUST LIFE HISTORY OF TREMATODES PLATE I

PLATE II

DESCRIPTION OF PLATE

Fig. 20.—*Cercaria pellucida*; sagittal section thru pharynx and gut of redia, with prepharynx organ retracted. × 330.

Fig. 21.—*Cercaria pellucida*; transverse section thru body in region of posterior locomotor pocket glands. × 170.

Fig. 22.—*Cercaria pellucida*; optical view of the proliferation of the germ-balls from the posterior germinal epithelium of the redia. × 330.

Fig. 23.—*Cercaria pellucida*; central nervous system, typical for the trioculate species of monostome cercariae. × 330.

Fig. 24.—Young *Cercaria pellucida*; oblique section thru ganglion mass, showing connection of eye-spots with brain center. × 330.

Fig. 25.—*Cercaria konadensis*; dorsal view. × 105.

Fig. 26.—Redia of *Cercaria konadensis*. × 34.

Fig. 27.—*Cercaria konadensis*; detail of paired group of caudal gland cells. × 540.

Fig. 28.—*Cercaria konadensis*; genital cell masses in region of ootype. × 540.

Fig. 29.—*Cercaria konadensis*; detail of excretory bladder and posterior locomotor pockets. × 238.

Fig. 30.—*Cercaria konadensis*; optical view of the germinal rachis of the redia. × 330.

Fig. 31.—*Cercaria konadensis*; sagittal section thru aspinose prepharynx of the redia. × 330.

Fig. 32.—Mature *Cercaria urbanensis* Cort; transverse section thru tail, showing caudal gland cells. × 330.

Figs. 33, 34.—*Cercaria urbanensis*; stages in differentiation of caudal gland cells from ordinary parenchyma cells. × 330.

Fig. 35.—*Cercaria urbanensis*; detail of excretory vesicle and posterior locomotor pockets. × 238.

Fig. 36.—Early germ-balls of *Cercaria urbanensis*; oblique section thru brain mass and lateral eye-spot, showing ectodermal origin of pigment cup, and connection with optic cells of brain. × 730.

Fig. 37.—Oblique longitudinal section thru *Cercaria pellucida*, showing detail of nerve endings. × 730.

20
le
cr
v
vf
vd
u
ov
ep
pgl
lp
25
cg
p
nc
r
26
lg
31
pa
cg
lm
32
lm
pa
cg
tr
27
l
pa
tr
33
pa
pgl
21
tr
l
cg
34
pa
gb
lg
e
l
ec
22
ut
vd
ve
vi
lc
ov
te
28
ev
epo
pgl
lp
35
ep
ev
pgl
lp
29
36
op
opc
opn
al
me
ad
lnc
av
br
le
pl
pd
pv
23
30
t
ec
lg
pa
op
opn
l
24
br
37
tr
lm
et
eg
ec
pa
ne
glc

PLATE III

DESCRIPTION OF PLATE

Fig. 38.—*Cercaria flabelliformis*; ventral view of worm freed from cyst; *ll*, lateral lappets × 80.

Fig. 39.—*Cercaria flabelliformis*; dorsal view, giving details of the excretory system and genitalia. × 80.

Fig. 40.—*Cercaria flabelliformis*; lateral view, showing suctorial cup in anterior portion of worm; *ll*, lateral lappets. × 80.

Fig. 41.—Immature *Cercaria flabelliformis* within cyst. × 54.

Fig. 42.—*Cercaria flabelliformis*; young redia, detailing the excretory channels in the worm. × 54.

Fig. 43.—*Cercaria flabelliformis*; redia showing paired salivary glands emptying into the oral pocket. × 54.

Fig. 44.—*Cercaria flabelliformis*; mid-frontal section thru young daughter redia in region of germinal cell maturation. × 330.

Fig. 45.—*Cercaria flabelliformis*; median frontal section thru young daughter redia, showing proliferation of germinal epithelium at posterior end of gut. × 330.

Fig. 46 a-m.—*Cercaria flabelliformis* rediae; maturation of parthenogenetic ova; *A*, resting cell; *B*, *C*, formation of spireme; *D*, division of spireme skein into eight chromosomes; *E*. *F*, *G*, longitudinal splitting of chromosomes at equatorial plate; *H*, mitosis, with forma. tion of polar body and preparation of ovum for second mitosis; *I*, polar body almost constricted off, chromosome *b* excentric; *J*, ovum preparing for second division, polar body also dividing; *K*, cell cleavage, with precocious chromosomes b_1, b_2 excentric; *L*, first cleavage of a cercaria-ovum, with polar body degenerating; *M*, metaphase of a somatic cell in process of division. × 1620.

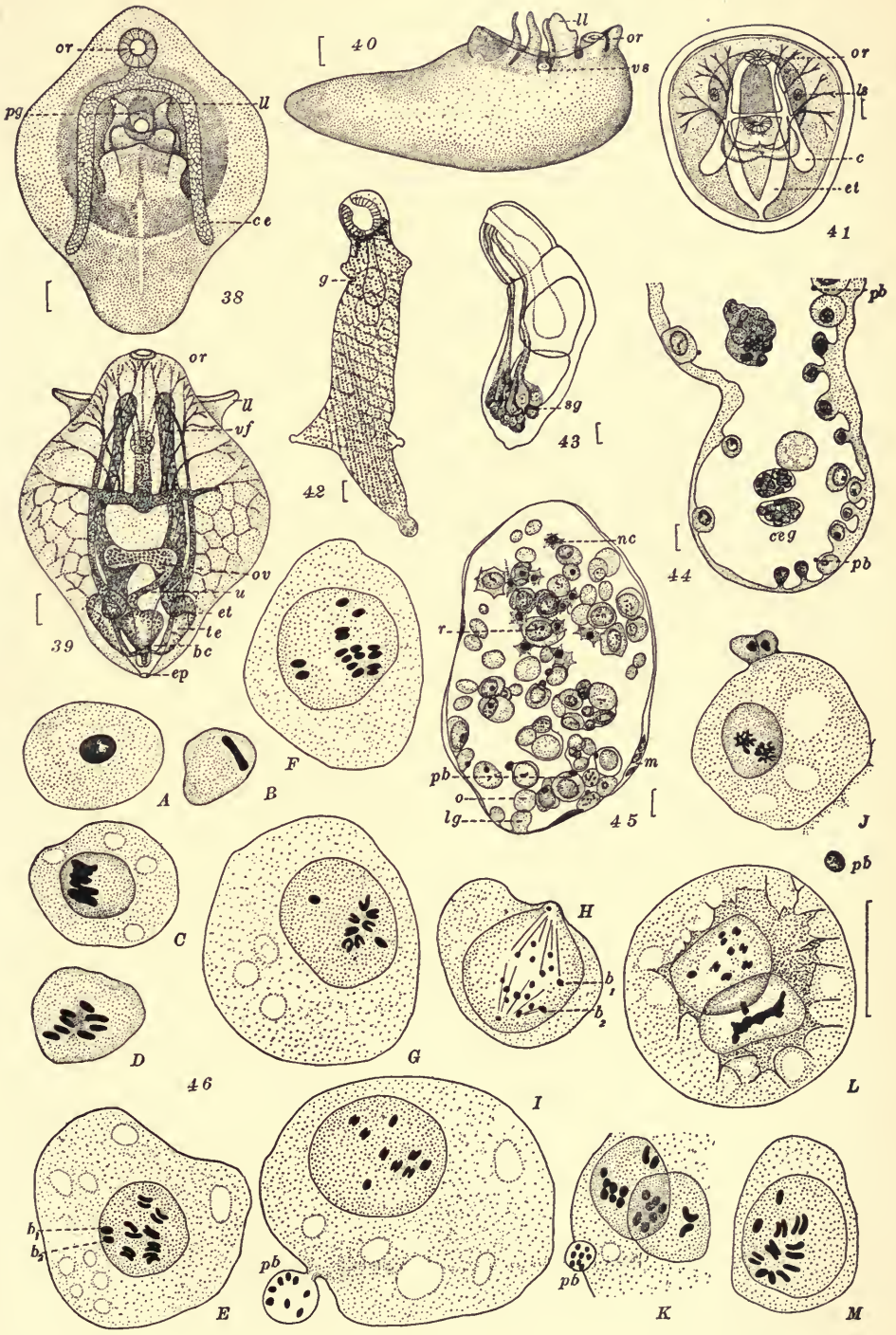

or
pg
ll
ce
38
ll
or
vs
40
or
ut
c
et
41
g
42
sg
43
pb
ceg
pb
44
or
ll
vf
ov
u
et
te
bc
ep
39
nc
r
m
pb
o
lg
45
A
B
F
J
pb
C
D
46
G
H
b1
b2
L
I
b1
b2
E
pb
pb
K
M

PLATE IV

DESCRIPTION OF PLATE

Fig. 47.—*Tetracotyle pipientis*; ventral view, showing digestive tract and genital system. × 105.

Fig. 48.—*Tetracotyle pipientis*; diagram of the excretory system, with excretory granular inclusions. × 105.

Fig. 49.—*Cercaria ptychocheilus*; ventral view, including digestive, excretory and genital systems. × 105.

Fig. 50.—*Cercaria ptychocheilus*; sketch of encysted worm. × 25.

Fig. 51.—*Cercaria ptychocheilus*; sketch of ruptured cyst with attachment annulus. × 25.

Fig. 52.—*Cercaria ptychocheilus*; detail of genital system. × 165.

Fig. 53.—*Cercaria ptychocheilus*; nervous system. × 330.

Fig. 54.—*Cercaria ptychocheilus*; transverse section thru middle of body. × 540.

Fig. 55.—*Cercaria crenata*; dorsal view. × 170.

Figs. 56, 57.—*Cercaria crenata*; ventral and lateral views of stylet. × 540.

Fig. 58.—*Cercaria crenata*; sporocyst. × 54.

Fig. 59.—*Cercaria crenata*; detail of genitalia. × 170.

Fig. 60.—*Cercaria glandulosa*; ventral view. × 370.

Fig. 61.—*Cercaria glandulosa*; ventral view of stylet. × 370.

Fig. 62.—*Cercaria glandulosa*; salivary and cystogenous glands. × 75.

Fig. 63.—*Cercaria glandulosa*; detail of caudal pockets, showing insertion of tail, spinose lateral grooves, and three-spined ventral flap. × 100.

Figs. 64, 65.—*Cercaria glandulosa*; outline of excretory vesicle, open and closed. × 200.

Fig. 66.—*Cercaria glandulosa*; genital cell masses, dorsal view. × 110.

Fig. 67.—*Cercaria glandulosa*; sporocyst. × 170.

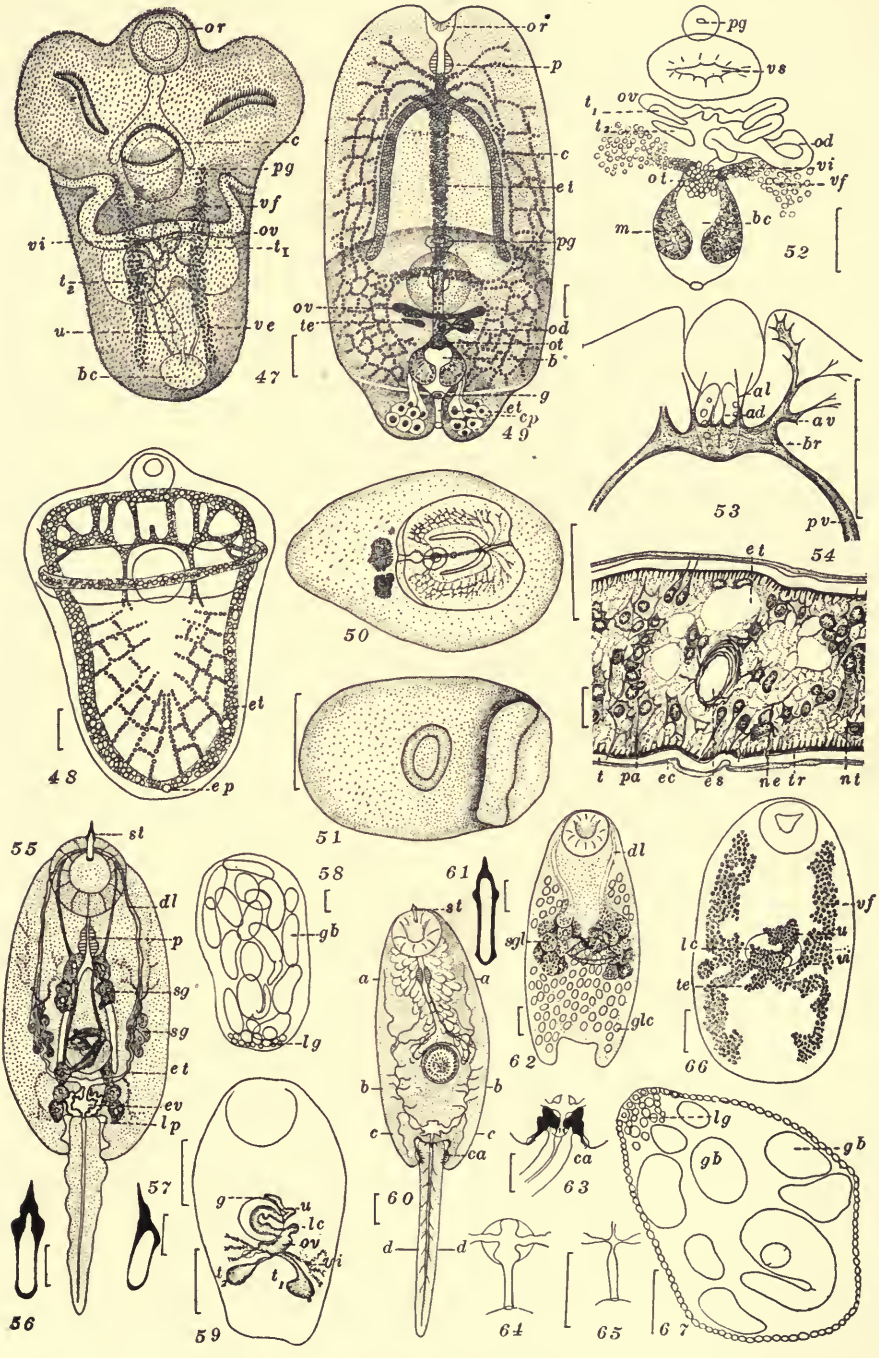

or
c
pg
vf
ov
vi
t_1
t_2
u
ve
bc
47
p
et
od
ot
b
g
cp
49
te
pg
vs
ov
t_1
t_2
od
vi
vf
ot
m
bc
52
al
ad
av
br
53
pv
et
54
t
pa
ec
es
ne
tr
nt
48
ep
50
51
55
st
dl
p
sg
sg
et
ev
lp
56
57
58
gb
lg
59
g
u
lc
ov
vi
t_1
t_2
61
st
a
a
b
b
c
c
ca
d
d
60
62
dl
syl
glc
63
ca
64
65
66
vf
u
vi
lc
te
lg
gb
gb
67

PLATE V

DESCRIPTION OF PLATE

Figs. 68-70.—*Cercaria glandulosa*; consecutive frontal sections, giving details of the nervous system anterior to the brain. × 540.

Fig. 71.—*Cercaria glandulosa*; frontal section, with details of innervation of acetabulum. × 540.

Fig. 72-75.—*Cercaria glandulosa*; transverse sections thru levels *aa* to *dd* of Fig. 60. × 540.

Fig. 76.—*Cercaria diaphana*; ventral view, considerably flattened by cover slip. × 170.

Fig. 77.—*Cercaria diaphana*; ventral view of stylet. × 540.

Fig. 78.—*Cercaria diaphana*; ventral view, giving details of glands and genital cell masses. × 170.

Figs. 79, 80.—*Cercaria diaphana*; sporocysts. × 80.

Fig. 81.—*Cercaria dendritica*; ventral view. × 170.

Figs. 82, 83.—*Cercaria dendritica*; lateral and ventral views of stylet. × 250.

Fig. 84.—*Cercaria dendritica*; encysted worm. × 150.

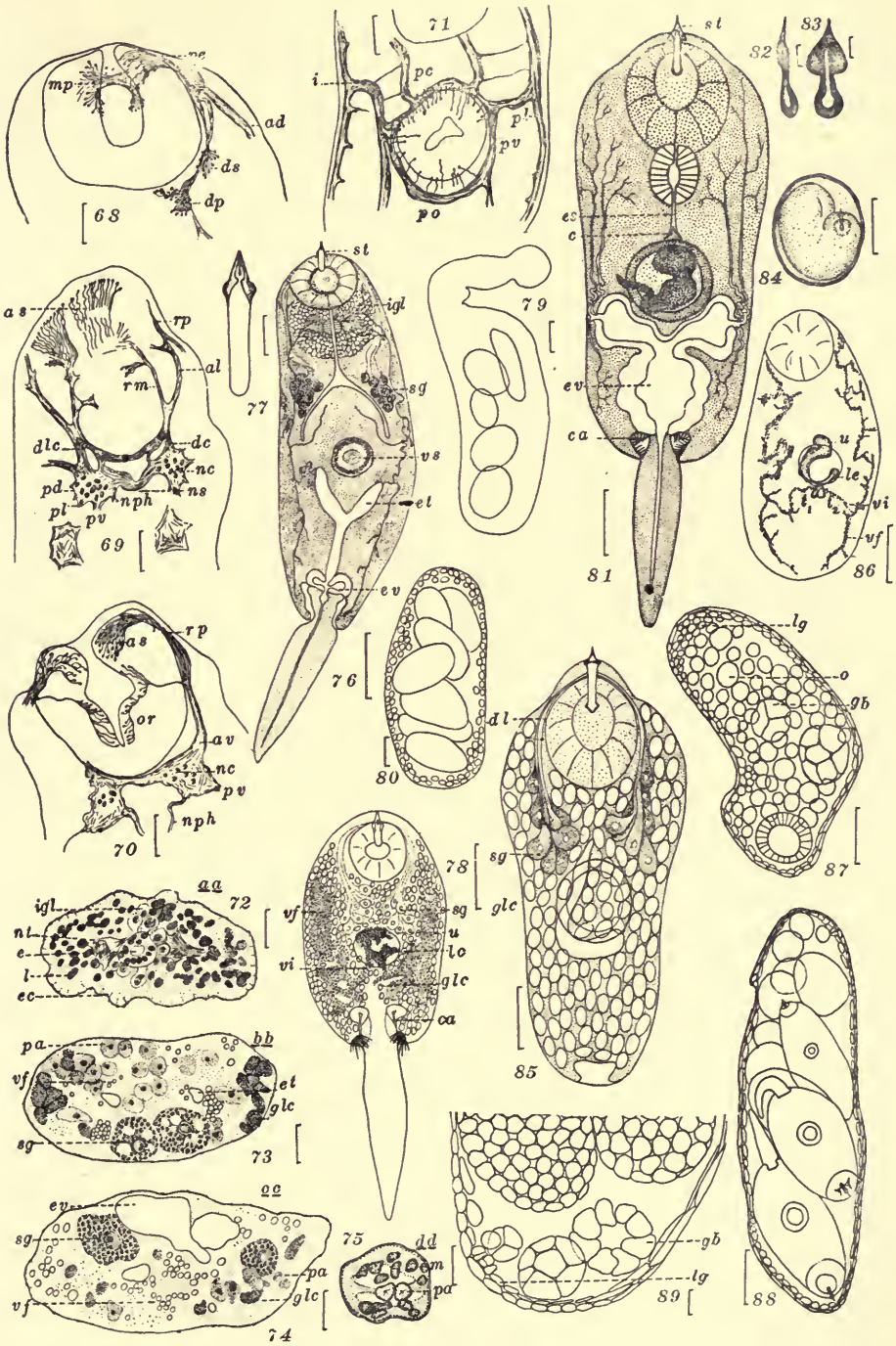
Fig. 85.—*Cercaria dendritica*; salivary and cystogenous glands. × 170.

Fig. 86.—*Cercaria dendritica*; genital system. × 150.

Fig. 87.—*Cercaria dendritica*; young sporocyst. × 150.

Fig. 88.—*Cercaria dendritica*; mature sporocyst. × 150.

Fig. 89.—*Cercaria dendritica*; posterior end of mature sporocyst, showing origin of germ-balls from localized germinal epithelium. × 330.



FAUST LIFE HISTORY OF TREMATODES PLATE V

PLATE VI

DESCRIPTION OF PLATE

Fig. 90.—*Cercaria micropharynx*; ventral view. × 170.
Figs. 91, 92.—*Cercaria micropharynx*; ventral and lateral views of stylet. × 540.
Fig. 93.—*Cercaria micropharynx*; distribution of glands. × 170.
Fig. 94.—*Cercaria micropharynx*; sporocyst with non-localized germinal epithelium. ×
Fig. 95.—*Cercaria micropharynx*; cercariae encysted in old sporocyst. × 54.
Fig. 96.—*Cercaria micropharynx*; genital cell masses. × 170.
Fig. 97.—*Cercaria micropharynx*; transverse section thru brain center. × 540.
Fig. 98.—*Cercaria micropharynx*; transverse section thru excretory cornua. × 540.
Fig. 99.—*Cercaria micropharynx*; transverse section thru tail. × 540.
Fig. 100.—*Cercaria racemosa*; ventral view. × 150.
Figs. 101, 102.—*Cercaria racemosa*; ventral and lateral views of stylet. × 330.
Fig. 103.—*Cercaria racemosa*; detail of salivary glands. × 150.
Fig. 104.—*Cercaria racemosa*; genital cell masses. × 330.
Figs. 105, 106.—*Cercaria racemosa*; sporocysts, showing localized germinal epithelium and attachment organ, *ao*. × 54.
Fig. 107.—*Cercaria racemosa*; lateral view of genital cell masses in region of acetabulum. × 330.
Fig. 108.—*Cercaria racemosa*; optical view of the sporocyst in region of birth-pore, *bp*; arrow points toward attachment organ. × 330.
Fig. 109.—*Cercaria trisolenata*; ventral view. × 150.
Fig. 110.—*Cercaria trisolenata*; dorsal view of collar spines. × 170.
Fig. 111.—*Cercaria trisolenata*; lateral view of collar spines. × 330.
Fig. 112.—*Cercaria trisolenata*; sketch of acetabular spines. × 540.
Fig. 113.—*Cercaria trisolenata*; typical cystogenous cell glands, showing granules and chromidia. × 540.
Fig. 114*A-E*.—*Cercaria trisolenata*; sketches of developmental stages. × 80.
Fig. 115 *A-C*.—*Cercaria trisolenata*; stages in encystment. × 80.

FAUST LIFE HISTORY OF TREMATODES PLATE VI

PLATE VII

DESCRIPTION OF PLATE

Fig. 116.—*Cercaria trisolenata*; encysted worm. × 150.
Fig. 117.—*Cercaria trisolenata*; redia. × 50.
Fig. 118.—*Cercaria trisolenata*; longitudinal and transverse muscle fibers of the digestive tract, showing myoblast connections. × 730.
Fig. 119.—*Cercaria trisolenata*; peripheral muscle fibers of longitudinal system. × 730.
Fig. 120.—*Cercaria trisolenata*; genital cell masses. × 220.
Fig. 121.—*Cercaria trisolenata*; butterfly stage in development of the central nervous system. × 330.
Fig. 122.—*Cercaria trisolenata*; differentiating stage in development of central nervous system. × 330.
Figs. 123, 124.—*Cercaria trisolenata*; lateral and dorsal views of central nervous system of mature cercaria. × 330.
Fig. 125.—*Cercaria trisolenata*; central nervous system of the redia. × 220.
Fig. 126.—*Cercaria trisolenata*; distribution of nerve cells in the redia, median sagittal section. × 330.
Fig. 127.—*Cercaria trisolenata*; detail of the peripheral nerves of the redia. × 540.
Figs. 128-133.—*Cercaria trisolenata*; transverse sections at levels *aa* to *ff* of Fig. 109. × 330.

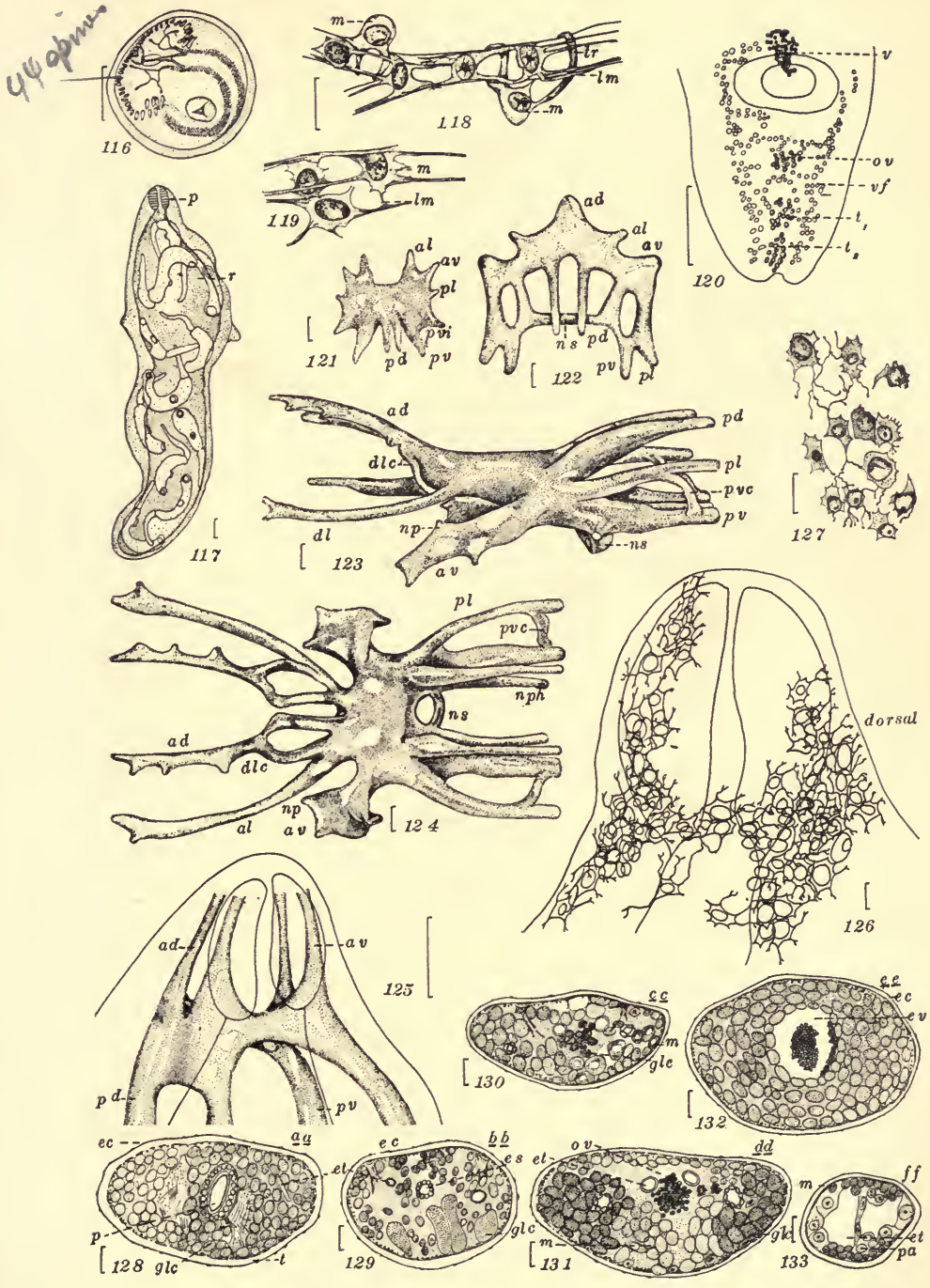
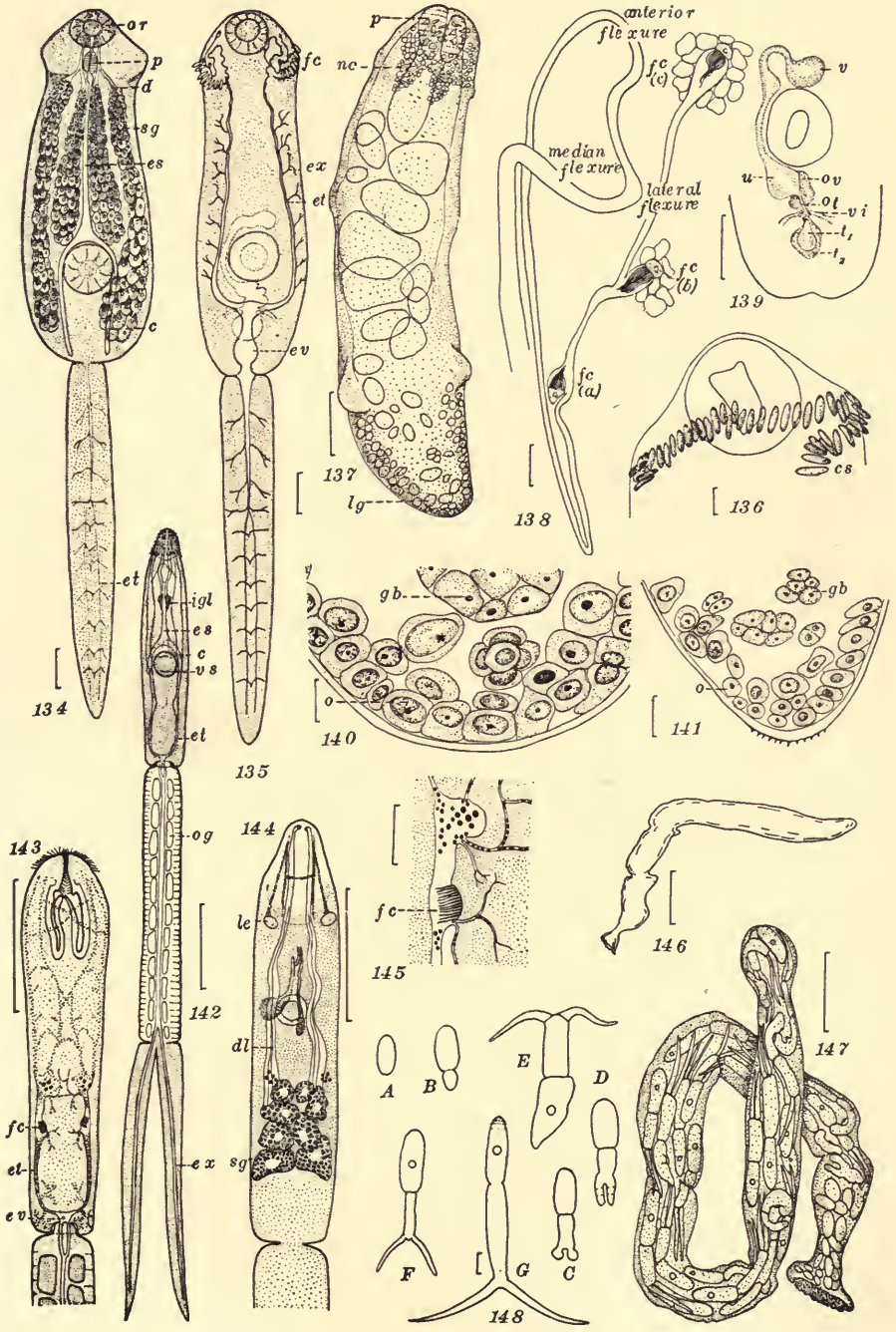

116
m
tr
lm
m
118
m
lm
119
v
ov
vf
t_1
t_2
120
p
r
117
al
av
pl
pvi
pd
pv
121
ad
al
av
ns
pd
pv
pl
122
ad
dlc
dl
np
av
pd
pl
pvc
pv
ns
123
127
pl
pvc
nph
ns
ad
dlc
al
np
av
124
dorsal
126
ad
av
pd
pv
125
ec
aa
et
p
t
128 glc
ec
bb
es
et
glc
129
ov
et
dd
m
glc
131
m
ff
et
pa
133
cc
m
glc
130
cc
ec
ev
132

PLATE VIII

DESCRIPTION OF PLATE

Fig. 134.—*Cercaria biflexa*; ventral view, showing salivary gland cells. × 105.
Fig. 135.—*Cercaria biflexa*: ventral view, showing excretory system. × 105.
Fig. 136.—*Cercaria biflexa*; lateral view of collar spines. × 330.
Fig. 137.—*Cercaria biflexa*; redia of worm. × 170.
Fig. 138.—*Cercaria biflexa*; detail of three flame cells in cephalic region. × 540.
Fig. 139.—*Cercaria biflexa*; genital cell masses. × 170.
Fig. 140.—*Cercaria trisolenata*; posterior end of redia. × 540.
Fig. 141.—*Cercaria biflexa*; posterior end of redia. × 540.
Fig. 142.—*Cercaria gracillima*; ventral view. × 230.
Fig. 143.—*Cercaria gracillima*; excretory system. × 350.
Fig. 144.—*Cercaria gracillima*; dorsal view of trunk, showing eye-spots and salivary glands × 350.
Fig. 145.—*Cercaria gracillima*; detail of flame cell of excretory system. × 750.
Figs. 146, 147.—*Cercaria gracillima*; sporocysts; Fig. 146, x 14; Fig. 147, × 21.
Fig. 148 *A-G*.—*Cercaria gracillima*; stages in development. × 50.



FAUST LIFE HISTORY OF TREMATODES PLATE VIII

PLATE IX

DESCRIPTION OF PLATE

Fig. 149.—*Cercaria gracillima*; genital cell masses. × 270.
Fig. 150.—*Cercaria gracillima*; nervous system. × 540.
Fig. 151.—*Cercaria gracillima*; central nervous system in a very young germ-ball. × 540.
Fig. 152.—*Cercaria gracillima*; transverse section thru esophagus glands. × 540.
Fig. 153.—*Cercaria gracillima*; transverse section thru region slightly posterior to that shown in Fig. 152. × 540.
Fig. 154.—*Cercaria gracillima*; transverse section thru salivary glands. × 540.
Fig. 155.—*Cercaria tuberistoma*; ventral view. × 170.
Fig. 156 *A-F*.—*Cercaria tuberistoma*; stages in development. × 75.
Figs. 157, 158.—*Cercaria tuberistoma*; sporocysts. × 54.
Fig. 159.—*Cercaria biflexa*; section thru liver tissue of *Physa gyrina* Say, showing infection; *a*, disintegrating cecum; *b*, broken down connective tissue; *c*, section of worm. × 170.
Fig. 160.—*Cercaria micropharynx*; section thru liver tissue of *Lymnaea proxima* Lea, infected with the worm; *a*, fatty bodies in degenerating cecum; *b*, vacuoles; *c*, sloughing tissue; *d*, karyolysis; *e*, section of worm. × 170.
Fig. 161.—*Cercaria gracillima*; section thru liver tissue of *Physa gyrina* Say infected with the worm; *a*, cytolysis; *b*, fatty globules; *c*, karyolysis; *d*, vacuoles; *e*, fibromata; *f*, sand inclusions; *g*, section of worm. × 240.

FAUST LIFE HISTORY OF TREMATODES PLATE IX

UNIVERSITY OF ILLINOIS-URBANA
570.5ILL C004
ILLINOIS BIOLOGICAL MONOGRAPHS URBANA
4 1917-18
3 0112 017753440